———. 1886. Studies in the botany of California and parts adjacent. Bulletin of the California Academy of Sciences 2:152.

- JUNAK, S., T. AYERS, R. SCOTT, D. WILKEN, and D. YOUNG. 1995. A flora of Santa Cruz Island. Santa Barbara Botanic Garden, Santa Barbara, California, and the California Native Plant Society, Sacramento, CA.
- MILLER, S. E. and W. S. DAVIS. 1985. Insects associated with the flowers of two species of *Malacothrix* (Asteraceae) on San Miguel Island, California. Psyche 92:547–555.
- MUNZ, P. 1974. A flora of southern California. University of California Press, Berkeley.
- PHILBRICK, R. N. 1972. The plants of Santa Barbara Island, California. Madroño 21(5), pt 2:329–393.
- RAVEN, P. H. 1963. A flora of San Clemente Island, California. Aliso 5:289-347.
- ROHLF, F. J. 1990. NTSYS-pc; numerical taxonomy and multivariate analysis system, ver. 1.6. Exeter Software, Setauket, New York.
- WALLACE, G. D. 1985. Vascular plants of the Channel Islands of southern California and Guadalupe Island, Baja California, Mexico. Natural History Museum of Los Angeles County, Contributions in Science 365.
- WILLIAMS, E. W. 1957. The genus *Malacothrix* (Compositae). American Midland Naturalist 58:494–517.

NOTEWORTHY COLLECTIONS

Arizona

CENTRANTHUS RUBER (L.) DC. (VALERIANACEAE).—Cochise Co., Bisbee, edge of parkinglot near junction of Main St. and Commerce St., 5400' (1620 m), 14 Oct 1996, Laferrière 2679. (ARIZ, ASU).

Previous knowledge. Eurasian species sometimes cultivated as an ornamental. Occasionally established in the wild in California (Munz & Kecky, 1959).

Significance. First time reported outside cultivation in Arizona.

SALPICHROA ORIGANIFOLIA (LAM.) BAILLON (SOLANACEAE)—Cochise Co., Bisbee, unkempt lawn at 129 Tombstone Canyon Road, 5400' (1620 m), 14 Oct 1996, Laferrière 2678 (ARIZ, ASU, MO).

Previous knowledge. Argentine species sometimes cultivated as an ornamental. Occasionally known from the wild in California and Florida but rarely producing fruit in North America (D'Arcy, MO, pers. comm.). The related *S. rhomboidea* (Gill. & Hook.) Miers is a difficult weed in parts of California (Munz & Keck, 1991).

Significance. First time reported outside cultivation in Arizona.

—JOSEPH E. LAFERRIERE, Herbarium, 113 Shantz Building, University of Arizona, Tucson AZ. 85721.

A NEW SUBSPECIES OF CLARKIA MILDREDIAE (ONAGRACEAE)

L. D. GOTTLIEB

Section of Evolution and Ecology, Division of Biological Sciences, University of California, Davis, CA 95616 ldgottlieb@ucdavis.edu

L. P. JANEWAY

Herbarium, Department of Biological Sciences, California State University, Chico, CA 95929

ABSTRACT

Clarkia mildrediae subsp. **lutescens** is a newly described subspecies that is readily distinguished from subsp. *mildrediae* by the color of its anthers which may be bright yellow, yellow-orange, light orange or red-orange on different plants while those of subsp. *mildrediae* are magenta. Subspecies *lutescens* has a separate and nonoverlapping geographical distribution primarily in Butte and Plumas Counties where subsp. *mildrediae* is also found. Within subsp. *lutescens*, the proportion of plants with bright yellow anthers varies among populations from 98% to none. Bright yellow is homozygous and true breeding and is allelic to red-orange. Plants from populations with high proportions of bright yellow anthers also have shorter and narrower petals. Hybrids between the two subspecies are fully fertile.

Heller (1940) first distinguished Clarkia mildrediae (Heller) Lewis and Lewis as Phaeostoma mildredae from P. atropurpureum Heller, later included in the widespread C. rhomboidea Douglas (Lewis and Lewis 1955), on the basis of its larger flowers and later flowering. Lewis and Lewis (1955) determined that P. mildredae (n =7) was one of the diploid parents of C. rhomboidea (the other being C. virgata Greene [n = 5]) and transferred it to Clarkia (Lewis and Lewis 1953). The relationship was proven by the finding (reported in Mosquin 1964) that experimental triploid hybrids between C. mildrediae and C. rhomboidea showed seven bivalents and five univalents at meiosis and those between C. virgata and C. rhomboidea showed five bivalents and seven univalents. The three species were recognized as Clarkia sect. Myxocarpa (Lewis and Lewis 1955). At that time, C. mildrediae was known only from a few localities on the North Fork of the Feather River in Butte and Plumas Counties and from the vicinity of Shasta Lake (Shasta County) to the north. Small (1971a, b) segregated the northern populations, by then extended to Trinity County, as C. borealis because of their virgate habit and lavender petals which differentiated them from C. mildrediae and because of the substantial differences between them in chromosomal arrangement which rendered their hybrids sterile. We

MADROÑO, Vol. 44, No. 3, pp. 245-252, 1997

MADROÑO

have been studying the species of sect. *Myxocarpa* (Gottlieb and Janeway 1995; Gottlieb and Ford unpublished) and our field work has led to the discovery of a new subspecies of *C. mildrediae* that we describe here as subsp. *lutescens*. The new subspecies has a separate and non-overlapping distribution, relative to subsp. *mildrediae*, in Butte and Plumas counties, and differs conspicuously in anther color and several other floral traits. Both subspecies are outcrossing and have the same chromosome number.

Anther color and genetics. Anthers of subsp. mildrediae are magenta and pollen is blue or blue-gray. Anthers of subsp. lutescens may be bright yellow, yellow-orange, light orange, or red-orange. Anther color is constant on each plant but may differ among plants within and between populations of subsp. lutescens (see below). In general, pollen color is correlated with anther color. Bright yellow anthers always have bright yellow pollen. Orange anthers are associated with tan or gray pollen, often with a yellow tinge, that sometimes darkens as the flower ages. Pollen of inner (epipetalous) anthers may initially appear yellow, darkening to tan, while pollen of the outer anthers may initially appear tan, darkening to a tangray, but never becoming blue or blue-gray. Anthers of subsp. lutescens are the same length as those of subsp. *mildrediae*, the outer ones generally 8-10 mm. They project forward of the four reddishpurple petals as in subsp. mildrediae, but their contrasting color, particularly when bright yellow, is an elegant and notable feature.

A preliminary genetic analysis of anther color has been carried out. Self-pollinated progeny of a plant grown from field-collected seed from subsp. *lutescens* population 4412 that had yellow-orange anthers and tan-yellow pollen showed bright yellow, yellow-orange, or orange anthers. Progeny with bright yellow and yellow-orange anthers were self-pollinated. Yellow-orange segregated progeny of three types: 13 bright yellow, 23 yellow-orange, and 12 orange anthers, suggesting that anther color in this cross was controlled by two alleles at a single locus and that the test plant was heterozygous. The progeny from plants with bright yellow anthers and pollen bred true, suggesting they were homozygous.

Experimental hybrids between subsp. *mildrediae* and subsp. *lutescens* have anthers and pollen of various colors depending on the allelic state of the controlling loci. To date, only a few crosses of this type have been grown. Magenta shows complete or incomplete dominance with orange and yellow in different crosses. The appearance of plants with magenta anthers and bright yellow pollen (a phenotype not observed in nature) in some progenies from intersubspecific crosses suggests that the color differences between the subspecies are governed by at least two loci.

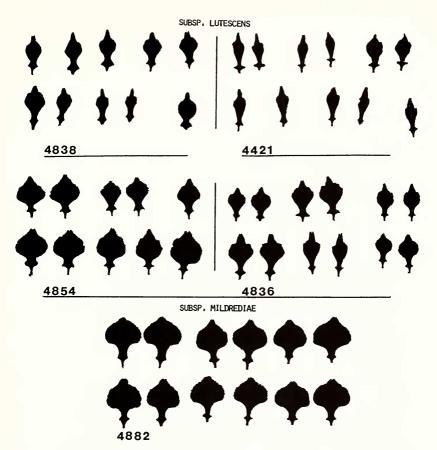


FIG. 1. Silhouettes of flower petals from representative populations of both subspecies of *C. mildrediae* grown in the greenhouse at Davis. For each plant, one petal was taken from both the first and second flower to open, on the day the stigma became receptive (usually three days after anthesis) because the petals are fully expanded then. The petals were placed on 3×5 cards under scotch tape which nicely preserves their size and shape. They were then xeroxed and the outlines filled in with black ink. Petals from five or six plants of each population are shown.

Petal shape. Petals of *C. mildrediae* have a deltoid or rounded limb that narrows into a claw with a pair of prominent lateral lobes above the slender base (Fig. 1). Petals from plants of numerous populations of both subspecies were measured in the field (Table 1) and also in the greenhouse (data not shown). Those of subsp. *mildrediae* are larger and broader. Within subsp. *lutescens*, plants from populations that have high proportions of light orange to red-orange anthers have nearly the same length and width as those of subsp. *mildrediae*. However, plants from populations that have predominantly bright yellow anthers and pollen, for example, populations

TABLE 1. PETAL LENGTH AND WIDTH COMPARISONS. Values reported (in mm) are means \pm 95% confidence limits for the population with the largest and the one with the smallest mean for each subspecies, with sample sizes in parentheses. Field measurements were of the second most recently opened flower which was generally one of the first three flowers on the inflorescence. The petals on each measured flower were fully expanded. Measurements were made in seven populations of *C. mildrediae* subsp. *mildrediae* and 13 of subsp. *lutescens*; sample sizes vary from 3 to 19 plants per population.

	subsp	o. lutescens	subsp.	mildrediae
Length	Pop. 4684	$20.5 \pm 1.0 (10)$	Pop. 4882	$21.1 \pm 0.6 (14)$
	Pop. 4837	$16.1 \pm 0.6 (10)$	Pop. 4681	$18.8 \pm 0.7 (14)$
	All pop.	$17.8 \pm 0.3 (130)$	All pop.	$20.1 \pm 0.3 (88)$
Width	Pop. 4693	$14.9 \pm 1.4 (10)$	Pop. 4882	$16.7 \pm 0.8 (14)$
	Pop. 4837	$7.7 \pm 0.9 (10)$	Pop. 4679	12.5 ± 1.1 (8)
	All pop.	$11.6 \pm 0.4 (130)$	All pop.	$14.9 \pm 0.5 (88)$

4421 and 4839 (Table 2), have shorter and significantly narrower petals (Fig. 1). The basis of this correlation has not yet been studied.

Geographical distribution. Clarkia mildrediae is distributed nearly entirely within Butte and Plumas Counties, with a few outlying locations in adjacent Yuba and Sierra Counties, east of Sly Creek Reservoir (Fig. 2). The subspecies are entirely allopatric and have not been found growing intermixed at any locality. Subspecies *lutescens* occurs in openings in the Yellow Pine forest and adjacent habitats from the North Fork of the Feather River, south and east of Pulga, and east to Big Creek (east of Bucks Lake) and south across the drainage of the Middle and South Forks of the Feather River to Canyon Creek, a tributary of the North Yuba River. Subspecies *mildrediae* occurs along the North Fork of the Feather River south of Belden, and north and west to the West Branch of the Feather River in the vicinity of Stirling City. Overall, its distribution is northwest of that of subsp. *lutescens*. In two areas, near Pulga on the North

Population	Number plants sampled	% bright yellow
4839	100	98
4421	50	98
4838	50	89
4429	41	34
4836	50	28
4854	108	3
4881	50	0
4687	40	0

TABLE 2. PROPORTION OF PLANTS WITH BRIGHT YELLOW ANTHERS AND POLLEN IN POPULATIONS OF *C. MILDREDIAE* SUBSP. *LUTESCENS*. Collections are those of LPJ.

1997]

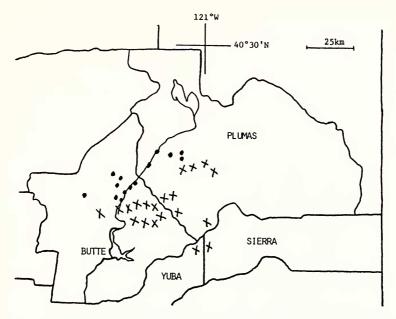


FIG. 2. Outline map of Butte, Plumas, and adjacent counties to show locations of collected populations of *C. mildrediae*. The North Fork of the Feather River is shown. Dots mark subsp. *mildrediae* and crosses mark subsp. *lutescens*.

Fork of the Feather River and southeast of Bucks Lake, populations of the two subspecies occur within several miles of each other.

In general, neither subspecies is known north or east of the vicinity of the Pacific Crest Trail in central Plumas County. Rainfall maps of the Plumas National Forest (Schultz and Benoit 1980) show that both subspecies are found in a region with mean annual precipitation greater than 145 cm; to the west and east of their distribution, the precipitation decreases rapidly. Both subspecies may be found in granitic, metamorphic or volcanic substrates and in elevations between 450 and 1700 meters.

As noted previously, populations of subsp. *lutescens* differ in the proportion of plants having different anther colors. Because bright yellow appears to be fully recessive to other colors and because this color can be readily identified, we scored the proportion of bright yellow in eight populations (Table 2). The proportion varied from 98% in populations 4421 and 4839 in the southwestern part of the distribution to zero or near zero in the northern and eastern portion. Populations that have predominantly bright yellow anthers seem to be restricted to Butte County.

Reproductive relationship. Pollen viability was examined in F_1 plants produced by crossing four pairs of populations representing

MADROÑO

the two subspecies. The F_1 plants were vigorous and more than 98% of their pollen was stainable with acetocarmine and had a normal three-pored appearance. The plants set abundant seed after experimental pollination. Thus, the subspecies are fully interfertile and there is no evidence that they differ in chromosomal arrangement.

Conclusions. Clarkia mildrediae subsp. *lutescens* is readily distinguished from subsp. *mildrediae* by the color of its anthers and by the narrower petals in populations that have a high proportion of bright yellow anthers. Subspecies *lutescens* has a separate and nonoverlapping geographical distribution in Butte and Plumas Counties where subsp. *mildrediae* is also found. The two have the same chromosome number and apparently the same chromosomal arrangement since their hybrids are fully fertile.

Subspecies *lutescens* was not recognized before now because previous students of *Clarkia* had not collected in its rugged territory. *Clarkia stellata* Mosquin, a predominantly self-fertilizing species that appears to have been derived from *C. mildrediae* (Mosquin 1962; Small 1971b) and is distributed in the same region of the northern Sierra Nevada, is probably derived from subsp. *lutescens* since both have yellow anthers and yellow pollen. We have designated the new taxon subsp. *lutescens* because the anthers, varying from bright yellow to red-orange on different plants, are its most distinctive feature.

TAXONOMY

Clarkia mildrediae (Heller) Lewis and Lewis subsp. lutescens Gottlieb and Janeway, subsp. nov.—TYPE: USA, California, Butte County, Plumas National Forest Road 28 at Chino Creek, 7 July 1995, *Janeway 4837* (Holotype, JEPS, Isotypes, CHSC, DAV, RSA).

A *C. mildrediae* (Heller) Lewis & Lewis subsp. *mildrediae* differt: antheris varians individuis luteis, flavis aurantiacis, aremeniacis, o rubris aurantiacis; petalorum limbo 7–16 mm lato.

Differs from *C. mildrediae* (Heller) Lewis & Lewis subsp. *mil-drediae:* anthers of different individuals yellow, yellow-orange, orange-red, or red; petal limbs 7–16 mm wide.

Paratypes. USA, California, Butte County, on road crossing (Plumas N.F. Road 28) of Last Chance Creek, 28 July 1982, *Schlising and Tarp 4358* (CHSC); along Bean Creek Road, ca. ³/₄ mi SW of Little Bald Rock, 29 June 1988, *Ahart 6102* (CAS, CHSC, MO); along French Creek Road 2.6 mi from Oroville-Quincy Hwy, 1 July 1993, *Janeway 4412* (CHSC, DAV); along French Creek Road 4.1 mi from Oroville-Quincy Hwy, 1 July 1993, *Janeway 4413* (CAS, CHSC); at the type locality Plumas N. F. Road 28 at Chino Creek,

2 July 1993, Janeway 4421 (CAS, MO); 1.3 mi S-SW of Hungry Hunt Peak, 2 July 1993, Janeway 4426 (CAS, CHSC); W end of Watson Ridge, 6 July 1993, Janeway 4429 (CHSC, DAV); between Haphazard Creek and Baker and Foreman Creeks, 7 July 1994, Janeway 4684 (CHSC); 1.3 mi S-SW of Hungry Hunt Peak, 7 July 1995, Janeway 4836 (GH, MO, RSA, US); along French Creek Road 4.1 mi from Oroville-Quincy Hwy, 7 July 1995, Janeway 4838 (LA, MO); between Mountain House, French Creek and Mosquito Creek, 7 July 1995, Janeway 4839 (HSC, NY, RENO, US); Plumas County. Oroville-Ouincy Hwy, 0.9 mi W of Grizzly Creek, 22 July 1993, Janeway 4469 (CHSC, DAV); Hartman Bar Ridge, 8 July 1994, Janeway 4687 (CHSC, DAV, JEPS, MO); between Lookout Rock and Middle Fork Feather River, 13 July 1994, Janeway 4693 (CHSC, JEPS); Oroville-Quincy Hwy, 0.9 mi W of Grizzly Creek, 29 July 1995, Janeway 4881 (CAS, MO, RSA, US); Sierra County. Rock Creek 0.3 mi NW of Canyon Creek, 1 July 1994, Janeway 4676 (CHSC); Yuba County. Slate Creek, 3 mi NE of Strawberry Valley, 1 July 1994, Janeway 4674 (CAS, CHSC); Slate Creek, 3 mi NE of Strawberry Valley, 15 July 1995, Janeway 4854 (GH, MO, RSA, US).

Collection numbers and localities of the populations of subsp. *mildrediae* cited in the text are identified below (all collections are those of Janeway): 4679: 0.7 mi E-SE of Flea Mountain (CHSC); 4681: Granite Ridge, along the Concow Road (CHSC); 4720: ¹/₄ mi W of Bear Ranch Creek Falls in North Fork Feather River Canyon; 4858: 0.8 mi NW of Oak Point (E of Stirling City) (CHSC, GH, NY, US); 4882: Pipeline Road, NW of Bucks Lake (CHSC, DAV, JEPS, RSA).

ACKNOWLEDGMENTS

We thank Kent Holsinger for assistance with the Latin diagnosis, and the curators of the following herbaria for loans of specimens and access to their collections: CAS, CHSC, DS, GH, JEPS, HSC, LA, MO, NY, OSC, POM, RENO, RSA, UC, US. This study was supported in part by the Plumas National Forest (LPJ) and by National Science Foundation grant BSR 91-06831 (LDG).

LITERATURE CITED

- GOTTLIEB, L. D. and L. JANEWAY. 1995. The status of *Clarkia mosquinii* (Onagraceae). Madroño 42:79–82.
- HELLER, A. A. 1940. New Californian plants. Leaflets in Western Botany 2:221.
- LEWIS, H. and M. E. LEWIS. 1953. New species and changes in nomenclature in the genus *Clarkia* (Onagraceae). Madroño 12:33–39.
 - —. 1955. The genus *Clarkia*. University of California Publications in Botany 20:251–392.
- MosQUIN, T. 1962. *Clarkia stellata*, a new species from California. Leaflets in Western Botany 9:215–216.

—. 1964. Chromosomal repatterning in *Clarkia rhomboidea* as evidence for post-pleistocene changes in distribution. Evolution 18:12–25.

- SCHULTZ, B. and T. BENOIT. 1980. Average annual precipitation. An overlay on the Plumas National Forest Map "based on Calif. Dept. of Water Resources Ppt., 1966." Quincy, CA. Unpublished. SMALL, E. 1971a. The systematics of *Clarkia* sect. *Myxocarpa*. Canadian Journal of
- Botany 49:1211-1217.

-. 1971b. The evolution of reproductive isolation in Clarkia sect. Myxocarpa. Evolution 25:330-346.

PHENETIC ANALYSIS OF *ARCTOSTAPHYLOS PARRYANA* I. TWO NEW BURL-FORMING SUBSPECIES

JON E. KEELEY Division of Environmental Biology, National Science Foundation, Arlington, VA 22230 jkeeley@nsf.gov

LAURA BOYKIN Department of Biology, San Francisco State University, San Francisco, CA 94132

> ALLEN MASSIHI Department of Biology, Occidental College, Los Angeles, CA 90041

Abstract

Arctostaphylos parryana Lemmon is here circumscribed as a species that includes both non-burl forming and burl-forming taxa. Principal components analysis based on 50 phenetic characters was used to support the recognition of two new subspecies. Arctostaphylos parryana subsp. tumescens Keeley, Boykin, & Massihi is morphologically similar to the nominate subspecies but is distinct in its geographical and ecological distribution, presence of a globose basal burl and erect growth form. Arctostaphylos parryana subsp. deserticum Keeley, Boykin, & Massihi also differs from the nominate subspecies in the presence of a basal burl, and differs from both other subspecies in its intensely glaucous, slightly narrower leaves and smaller fruits and desert chaparral habitat. These subspecies increase the range of *A. parryana* by >150 km southeastward, and to the San Bernardino, San Jacinto, Santa Rosa, and San Ysidro mountain ranges and to Riverside and San Diego counties.

As presented in previous taxonomic treatments, *Arctostaphylos parryana* Lemmon is a polyploid, non-burl forming manzanita with a mounded growth form (Fig. 1) and typically is distributed as scattered shrubs in arid woodlands and montane forests (Adams 1940, Wells 1993). It ranges from Lockwood Valley and Mt. Pinos in eastern Ventura County to the southern Tehachipi Mountains of Kern County and northern and eastern portions of the San Gabriel Mountains in Los Angeles and San Bernardino counties. It is morphologically distinguished by its tomentose branchlets and rachises, reduced floral bracts, and round fruits with a solid endocarp stone. Recently we have made extensive collections of manzanitas with these characteristics, indicating clear affinities to *A. parryana*, and in this paper we will show

(1) A significant increase in the range of this species east and south,

MADROÑO, Vol. 44, No. 3, pp. 253-267, 1997



FIG. 1. Mounded growth form of typical A. parryana.

- (2) that the species includes many burl-forming populations,
- (3) these populations are best treated as subspecies, and in a subsequent contribution (Keeley et al. in preparation) we will show
- (4) The pattern of variation in *A. parryana* suggests the hypothesis that there has been widespread hybridization and introgression from *A. glandulosa* Eastwood, and
- (5) evidence that A. gabrielensis Wells comprises a single population along a cline from A. parryana to A. glandulosa.

STUDY SITES

Distribution of taxa considered here is shown in Figure 2 and names, locality data, and sample sizes are in Table 1. Here the term "population" is used broadly to refer to both distinct populations as well as metapopulations (groups of populations separated by areas of unsuitable habitat).

METHODS

Extensive collections of all populations were made in late summer and autumn in order to obtain both current-year fruits and nascent inflorescenses for the following year. These are critical characters in manzanita taxonomy and only specimens with both present were included in our phenetic analysis. The combined presence of these two characters was a determining factor in the final sample size for

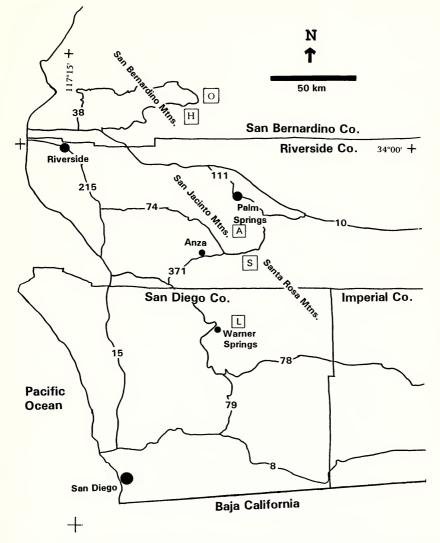


FIG. 2. Eastern distribution of populations studied here. See Table 1 for location data and sample sizes.

each population. A total of 50 characters were recorded for each plant sample, which were subsequently retained as vouchers and deposited at RSA. Fifteen quantitative, 2 meristic, and 30 qualitative characters, and 3 calculated ratios were recorded from each specimen. Qualitative characters were ranked from 1 to 5. Quantitative characters were represented by the mean of two samples from each

	-	Sample	- c		C SW	T	
	Code	SIZE	Burl	County or Country	Mtn. Kange	Location	Elevation (m)
A. parryana							
"Ventura"	^	39	No	Ventura/Kern	Tehachapi	Lockwood Valley	1500-1700
					& Mt. Pinos	Mutau Flat	1500-1700
					region	Mt. Pinos	1900
						Cero Noroeste	1900-2400
"San Gabriels"	50	68	No	Los Angeles	San Gabriel	Sulphur Spgs.	1600-1700
				& San Bernardino		Wrightwood	2000
						Pacifico	2000
						Crystal Lake	1850
						San Antonio Cyn	1900
"Onyx"	0	59	No	San Bernardino	San Bernardino	NE Onyx Peak	2400
						Rattlesnake Cyn	2100
"Heartbar"	Η	58	Yes	San Bernardino	San Bernardino	SW Heartbar Pk	2100–2300
"Andreas"	A	20	Yes	Riverside	San Jacinto	Andreas Cyn	2000-2100
"Santa Rosa"	S	<u>66</u>	Yes	Riverside	Santa Rosa	N/W Sta. Rosa Mtn.	1600-2200
"Los Coyotes"	L	30	Yes	San Diego	San Ysidro	Borrego-Palm Cyn	1300-1700
				I		Indian Cyn	
A. peninsularis	R	20	Yes	Baja California	San Pedro Martir	W of National Park	1000 - 2000
A. glandulosa	J	30	Yes	San Diego	San Marcos	Encinitas-Econdido	100-500

TABLE 1. POPULATIONS OF ARCTOSTAPHYLOS INCLUDED IN THIS STUDY.

256

[Vol. 44

specimen. All character states were standardized by transforming each variable with a z-score obtained by subtracting each observation from the mean of all individuals, and dividing by the standard deviation. This data matrix was used for ordination with principal components analysis using SYSTAT for Windows, Version 5.05 (Evanston, IL).

Stomatal density on ad- and abaxial surfaces were determined on a sub-sample from each population from epidermal peels made of clear nail polish and examined under $40 \times$. Since there was relatively little inter-population variability these data were not taken from every specimen and were not used in the principal components analysis. Chromosome counts were made on some populations from flower buds collected in late winter to early spring and preserved in 3:1 ethanol:glacial acetic acid. Anthers, not yet pigmented, were dissected out and squashed with aceto-carmine and examined at $100 \times$. This character was likewise not used in the principal components analysis. Additionally, characters with zero variance were automatically excluded from the principal components analysis.

RESULTS

San Bernardino Mountains. Although previously unrecorded from this range, there is an extensive population of A. parryana between 2100 and 2300 m on the western and southern slopes of Heartbar Peak (Table 1 and Fig. 2). These plants are approximately 80 km E of the known range of A. parryana in San Antonio Canyon in the San Gabriel Mountains. They are clearly related to A. parryana in their bright green foliage, tomentose branchlets and rachises, and relatively large round glabrous fruits with a solid stone (Fig. 3). However, the Heartbar Peak population differed significantly in that each shrub had a well-developed basal burl and lacked the mounded growth form of typical A. parryana. Further, the population covered several hectares of densely packed erect manzanitas in association with other chaparral shrubs. This contrasts sharply with the mounded growth form and scattered distribution in woodland and forest gaps, typical of non-burl forming A. parryana. The Heartbar population is largely restricted to chaparral on steep slopes and is replaced by A. patula in forest gaps in the valley bottom.

Principal components analysis comparing the phenetic traits (excluding the burl and growth form characters) of this Heartbar Peak population (H) with typical *A. parryana* from Ventura County (v) and the San Gabriel Mountains (g) (see Table 1 for location data) verifies the morphological similarity between the newly discovered Heartbar population and typical *A. parryana* (Fig. 4). Although these populations overlapped a great deal, there was some separation along the factor 1 axis, which accounted for 11% of the total vari-



FIG. 3. Large round glabrous fruits of the Heartbar A. parryana.

ance. Based on the component loadings, which indicate the extent each character contributes to the variance, the primary difference between these populations was the slightly sparser pubescence and somewhat larger fruits in the Heartbar population. Despite the phenetic similarity, the Heartbar manzanitas were clearly distinguishable from typical *A. parryana* by the prominent basal burl, erect growth habit, and affinity for chaparral.

On the eastern face of the San Bernardino Mountains, between 2100 and 2400 m, a widely scattered population of non-burl forming *A. parryana* was also collected, E of Onyx Peak and extending several km N to Rattlesnake Canyon (Table 1 and Fig. 2). As with

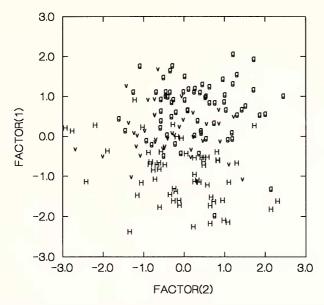


FIG. 4. Plot of the first two factors in the principal component analysis comparing the burl-forming Heartbar manzanitas (H), and typical non-burl-forming *A. parryana* from Ventura County (v) and the San Gabriel Mountains (g). See Table 1 for locations and sample sizes and Table 2 for factor 1 loadings, which explained 11% of the total variance.

typical *A. parryana*, these plants had a mounded growth form and generally were associated with pinyon-juniper woodland. Principal components analysis showed that these manzanitas (o) were largely indistinguishable from typical *A. parryana* from Ventura County (v) and the San Gabriel Mountains (g) (Fig. 5). Separation along the factor 1 axis accounted for 12% of the total variance, primarily contributed by slightly larger fruits in the Onyx populations. Otherwise, this population greatly resembled typical *A. parryana*, however, it represents approximately a 100 km eastward range extension for *A. parryana*.

San Jacinto, Santa Rosa, and San Ysidro ranges. Burl-forming manzanitas with tomentose branchlets, reduced floral bracts, and round solid fruits, indicating affinities to *A. parryana*, are also found in three mountain ranges south of the San Bernardino Mountains (Table 1 and Fig. 2). All of these populations occur in chaparral near the desert edge and many are accessible only by trail.

The most extensive populations we have found to-date are at the northern end of the Santa Rosa Mountain Range (Riverside County), between 1600 and 2200 m, on the western and northern sides of Santa Rosa Mountain. Principal components analysis (not shown)

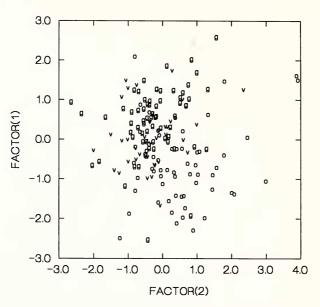


FIG. 5. Plot of the first two factors in the principal component analysis comparing the non-burl-forming *A. parryana* populations from Ventura County (v), San Gabriel Mountains (g), and E of Onyx Peak in the San Bernardino Mountains (o). See Table 1 for locations and sample sizes and Table 2 for factor loadings; factor 1 explained 12% of the total variance.

of four widely separated populations on Santa Rosa Mountain indicated extensive morphological overlap between these populations, thus all populations were treated together as a metapopulation.

Principal components analysis showed that the burl-forming Santa Rosa Mountain (S) manzanitas are well separated from the non-burl forming Ventura (v) plants and overlap slightly with the burl-forming Heartbar (H) plants (Fig. 6). The Santa Rosa Mountain manzanitas share with the Heartbar plants the erect habit and basal burl but differ in having markedly smaller fruits and a preponderance of plants with very glaucous-white leaves, as indicated by the component loadings (Table 2). Overlap between the Santa Rosa Mountain and Heartbar populations (Fig. 6) is due to weakly glaucous shrubs at the higher elevations on Santa Rosa Mountain.

Other extensive burl-forming populations with affinities to *A. parryana* occur further south in the San Ysidro Mountains on the eastern border of the Los Coyotes Indian Reservation in San Diego County (L). These plants appear similar to the Santa Rosa Mountain plants but are strikingly unlike the Heartbar plants in their intensely glaucous and narrower leaves and smaller fruits. Principal components analysis indicates that the Los Coyotes populations are clearly separable from the

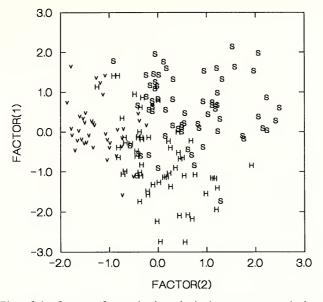


FIG. 6. Plot of the first two factors in the principal component analysis comparing the burl-forming Santa Rosa Mountain population (S) with the burl-forming Heartbar (H), and non-burl-forming Ventura County (v) and the San Gabriel Mountains (g) *A. parryana*, See Table 1 for locations and sample sizes and Table 2 for factor 1 loadings, which explained 10% of the total variance.

typical non-burl-forming *A. parryana* from Ventura County and distinct from the burl-forming *A. parryana* from Heartbar in the San Bernardino Mountains (Fig. 7). The factor 1 axis accounts for 17% of the total variance and component loadings indicate that shorter bract length and greater leaf glaucousness and scabrousness are most significant in separating these populations (Table 2).

Burl-forming *A. parryana* also occur on the desert slopes of the San Jacinto Mountains. One population from Andreas Canyon (A) more resembled Santa Rosa and Los Coyotes plants than San Bernardino plants. Principal components analysis (not shown) indicated that these manzanitas were clearly separable from the Heartbar population and Ventura County population, and the factor 1 axis accounted for 21% of the total variance.

Comparison with other Arctostaphylos *species*. Several characteristics of these burl-forming *A. parryana* populations, e.g., round glabrous fruits with solid stones and glaucous leaves, burls, and desert affinity in some, are shared with the northern Baja California *A. peninsularis* Wells. These *A. parryana* populations also share the burl-forming habit with the widespread coastal range species *A. glandulosa*. Principal components analysis comparing the burl-form-

Character	Fig. 4	Fig. 5	Fig. 6	Fig. 7	Fig. 8
Burl	N.I.	N.I.	0.193	0.284	 N.I.
Leaf blade length	-0.132	-0.090	-0.155	0.243	0.356
Leaf blade width	0.066	0.425	-0.415	-0.188	-0.005
Ratio leaf width/length	-0.219	-0.512	0.415	0.462	0.005
Basal angle	-0.141	-0.474	0.128	0.462	0.430
Apical angle	-0.141 -0.156	-0.474 -0.431	0.128	0.200	0.218
Blade shape	0.053	-0.431 -0.327	0.221	-0.214	0.240
Petiole length	-0.250	0.061	-0.026	0.192	0.030
Leaf color	-0.570	-0.394	0.020	0.315	0.020
Leaf glaucousness	0.003	-0.158	-0.571	-0.816	-0.088
Leaf scabrousness	-0.302	-0.143	0.399	0.310	0.088
Branchlet pubescence	-0.502	-0.143 -0.550	0.378	0.764	0.890
Petiole pubescence	-0.624	-0.530 -0.572	0.378	0.682	0.890
	-0.024	-0.572	0.190	0.082	0.001
Leaf blade pubescence Mature leaf	-0.307	-0.207	0.432	0.300	0.765
Immature leaf	-0.307	-0.207 -0.309	0.432	0.500	0.703
	-0.511	-0.309 -0.467	0.203	0.379	0.812
Rachis pubescence	-0.0370	-0.467 -0.081	0.380	0.728	0.830
Pedicel pubescence		0.232	0.321	0.012	0.817
Branchlet glandularity	0.503		0.131	0.478	0.885
Petiole glandularity	0.147 N.I.	-0.023 N.I.	0.187	0.387	0.910
Leaf blade glandularity					
Rachis glandularity	0.464	0.163 N.I.	0.183	0.258 0.466	$0.876 \\ 0.887$
Pedicel glandularity	0.176		0.377		
Inflorescence length	0.063	0.201	0.154	0.020	0.237
# of rachis branches	0.513	0.269	-0.132	-0.142	-0.023
Bract spacing	0.503	0.176	-0.245	-0.156	-0.042
Bract keel	0.127	0.289	0.057	0.185	-0.602
Bract shape	0.166	0.132	-0.057	-0.236	-0.781
Bract marcescence	-0.417	-0.301	-0.287	0.239	-0.276
Bract reflexed	-0.079	-0.093	-0.037	0.407	0.574
Bract length, subtending	0.120	0.170	0.000	0.951	0 (22
Inflorescence	-0.128	0.170	0.609	0.851	0.622
Flower bud	-0.329	-0.139	0.161	0.104	0.674
Pedicel length	-0.269	0.160	0.011	0.480	-0.037
Sepal shape	-0.364	-0.296	0.420	-0.015	-0.617
Sepal reflexed	0.071	0.022	0.342	0.487	-0.119
Fruit color	0.084	-0.033	-0.003	0.517	-0.170
Fruit height	0.307	0.525	-0.519	-0.406	-0.727
Fruit width	0.477	0.599	-0.607	-0.305	-0.438
Fruit width/fruit height	0.147	0.061	-0.103	0.200	0.585
Fruit weight	0.477	0.700	-0.706	-0.482	-0.597
Fruit pubescence	0.181	0.094	0.044	0.588	0.486
Fruit glandularity	N.I.	N.I.	0.171	0.267	0.723
Pericarp weight	0.453	0.530	-0.399	-0.277	-0.507
Endocarp weight	0.469	0.599	-0.707	-0.493	-0.541
Endocarp height	0.400	0.466	-0.472	-0.159	-0.677
Endocarp width	0.510	0.566	-0.661	-0.322	-0.563
Endocarp apiculate	-0.229	-0.199	-0.011	-0.089	-0.590
Mesocarp texture	0.170	0.174	-0.115	-0.157	-0.370
Endocarp segments	-0.305	-0.286	0.128	0.296	0.710
Endocarp lateral ridges	-0.433	-0.463	0.027	0.063	-0.190
Endocarp sculpturing	-0.287	-0.332	0.035	0.016	-0.439

TABLE 2. CHARACTERS USED IN PRINCIPLE COMPONENTS ANALYSIS AND COMPONENT LOADINGS FOR FACTOR 1 FOR FIGURES 4, 5, 6, 7, & 8. N.I. = not included.

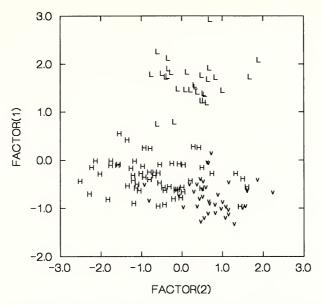


FIG. 7. Plot of the first two factors in the principal component analysis comparing the burl-forming Los Coyotes population (L) with the burl-forming Heartbar (H), and non-burl-forming Ventura County (v) *A. parryana.* See Table 1 for locations and sample sizes and Table 2 for factor 1 loadings, which explained 17% of the total variance.

ing A. parryana taxa (H,A,S,L) with burl-forming A. peninsularis (R) from the San Pedro Mártir and A. glandulosa (C) from the coastal ranges of San Diego County is shown in Figure 8. The strongest separation was on the factor 1 axis, which accounted for 33% of the variance and illustrates that these A. parryana taxa are clearly distinct from A. glandulosa and A. peninsularis, based largely on indument and fruit characters (Table 2).

Chromosome number. Two chromosome counts on the burl-forming Heartbar A. *parryana* gave counts of n = 26, indicating they were tetraploid. Two counts for non-burl-forming Onyx Peak and Rattlesnake Canyon specimens likewise gave counts of n = 26, and one count for a Santa Rosa Mountain plant gave a count of n = 26. Three counts for Los Coyotes plants gave both n = 13 and n = 26.

DISCUSSION

These studies greatly change our perception of *A. parryana*, in terms of its geographical range, ecology, and range of phenetic variation. The Heartbar population is morphologically quite close to the type, although fruits are somewhat larger (Fig. 3). This population

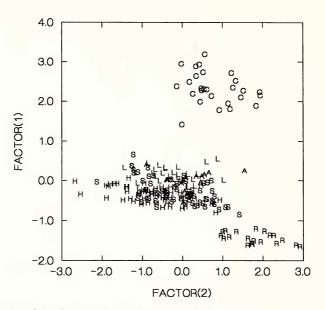


FIG. 8. Plot of the first two factors in the principal component analysis comparing the burl-forming populations of *A. parryana* (H = Heartbar, S = Santa Rosa, L = Los Coyotes, A = Andreas Cyn) with the burl-forming *A. glandulosa* (C) and burl-forming *A. peninsularis* (R). See Table 1 for locations and sample sizes and Table 2 for factor 1 loadings, which explained 33% of the total variance.

is markedly unlike typical *A. parryana* in having a well-developed basal burl, an erect growth form and distribution in dense montane chaparral. This contrasts markedly with *A. parryana* throughout its range where it is a non-burl-forming shrub with a mounded growth form (Fig. 1) and is distributed as scattered shrubs, in pinyon-juniper woodland or mixed conifer forests. We believe these differences are significant and the San Bernardino Mountains burl-forming plants should be recognized at the level of subspecies.

Burl-forming A. parryana in the ranges south of the San Bernardino Mountains are, however, phenetically quite distinct from the Heartbar population, most prominently in their intensely glaucous foliage, and they also have slightly narrower and more pointed leaves, and smaller fruits. Additionally, this taxon is ecologically distinct in its restriction to chaparral on the desert edge of the San Jacinto, Santa Rosa, and San Ysidro mountains. Therefore, we propose these glaucous-leaved manzanitas be treated as an additional subspecies.

TAXONOMIC TREATMENT

Arctostaphylos parryana subsp. tumescens J. Keeley, Boykin, & Massihi, subsp. nov.—TYPE: USA, California, San Bernardino County, chaparral covered slopes on NW face of Heartbar Peak, S of Hwy 38, 2160 m, San Bernardino Mountains, 34°10', 116°45', 23 Sept 1992, *J. Keeley & M. Keeley 21436* (holotype, RSA; isotypes, CAS, SD, MO).

Frutices erecti, caudex tumescens, repullulans post combustum; drupae 10 mm diametro.

Erect shrub with large globose burl formed early in development and platform-like on older resprouted shrubs, in chaparral habitat. Fruits 10 mm diameter. n = 26 (A. Massihi and J. Keeley). The epithet recognizes the swollen basal burl.

Montane chaparral in eastern San Bernardino Mountains, from Heartbar Peak east, and in the San Gabriel Mountains, such as chaparral near Newcomb Ranch (*J. Keeley 20599*, RSA).

Paratypes. USA, California, San Bernardino County, Rd to Coon Crk., 5.0 km SE of Hwy 38, southern base of Heartbar Peak, 2310 m, 27 Sept 1992, *J. Keeley 21864* (RSA); ecotone of chaparral and *Quercus chrysolepis* woodland, SE face of Heartbar Peak, 2250 m, 25 October 1992, *J. E. Keeley 22305* (RSA).

Arctostaphylos parryana subsp. deserticum J. Keeley, Boykin, & Massihi, subsp. nov.—TYPE: USA, California, San Diego County, Middle Fork Borrego Palm Cyn., 3–4 km SE San Ignacio, E of Hot Springs Mountain, 1500 m, San Ysidro Mountains, 33°17', 116°30', 26 Sept 1992, J. Keeley 21656 (holotype, RSA; isotypes, CAS, SD, MO).

Frutices erecti, caudex tumescens, repullulans post combustum; laminae glaucae, ellipticae, apices acuti; drupae 7–8 mm diametro.

Erect shrub with large globose burl formed early in development and platform-like on older resprouted shrubs, in chaparral near desert edge. Leaf blades narrow-elliptic with acute apices and moderately to intensely glaucous, fruits 7–8 mm diameter. n = 13, 26 (A. Massihi and J. Keeley). The epithet recognizes the consistent tendency of this taxon to be restricted to the desert edge of chaparral.

Chaparral at desert edge in San Diego and Riverside counties.

Paratypes. USA, California, San Diego County, Los Coyotes Indian Reservation, Indian Canyon, E. of Warner Springs, 1320 m, 10 April 1994, *Massihi, J. Keeley 25300* (RSA); S facing slopes E of Hot Springs Mountain, upper end of Choke Cherry Valley, Los Coyotes Indian Reservation, 1670 m, 18 September 1992, *J. Keeley 21326* (RSA); Riverside County, Road to Santa Rosa Mountain (7SO2), 2.5 km S of Hwy 74, 1640 m, Santa Rosa Mountains, 32°00', 116°30', 16 July 1992, *J. Keeley 16636* (RSA).

Character	A. parryana ssp. parryana	A. parryana ssp. tumescens	A. parryana ssp. deserticum	A. glandulosa (coastal San Diego)	A. peninsularis (San Pedro Martir)
Sample size	107	58	30	33	20
Chromosome #	n = 26	n = 26	n = 13, 26	n = 26	i
Burl	No	Yes	Yes	Yes	Yes
Leaves					
Length	32 ± 1	32 ± 1	33 ± 1	37 ± 1	32 ± 1
Length/width	1.6 ± 0.0	1.5 ± 0.0	1.7 ± 0.0	1.8 ± 0.1	1.7 ± 0.0
Apical angle	39 ± 1	34 ± 1	44 ± 1	46 ± 2	44 ± 1
Glaucous	4.1 ± 0.1	4.0 ± 0.1	2.1 ± 0.1	2.8 ± 0.1	1.3 ± 0.1
Scabrous	1.2 ± 0.1	1.0 ± 0.1	2.2 ± 0.1	2.6 ± 0.2	1.0 ± 0.0
Stomata					
Abaxial density					
$(\#/mm^2)$	24 ± 0	25 ± 0	21 ± 0	27 ± 1	25 ± 1
Ratio					
abaxial/adaxial	1.0 ± 0.0	1.1 ± 0.0	1.0 ± 0.0	1.4 ± 0.1	1.2 ± 0.1
Branchlet indument	Tomentose	Tomentose	Tomentose	Hirsute	Glabrous
				Eglandular to intensely glandular	
Lower Bract				microsoft Elandara	
Length	0.4 ± 0.1	0.1 ± 0.1	4.6 ± 0.2	6.3 ± 0.4	0.2 ± 0.2
Fruits					
Width/height	1.0 ± 0.0	1.0 ± 0.0	1.1 ± 0.0	1.5 ± 0.1	1.0 ± 0.0
Mass (g)	383 ± 9	447 ± 19	329 ± 17	145 ± 10	242 ± 19
Pvrenes	12 + 00	11 + 0.0	13 + 01	31 + 0.0	10 + 00

266

1997]

CONCLUSIONS

Table 3 contrasts these newly described subspecies with Arctostaphylos parryana ssp. parryana and with other morphologically similar burl-forming species. Morphologically, A. parryana ssp. tumescens is nearly indistinguishable from the nominate subspecies and has diverged largely in habitat, growth form and the presence of a basal burl. Greater divergence is seen in A. parryana ssp. deserticum with several foliage characteristics tending towards those of A. glandulosa, with which it co-occurs on the western edge of its range. However, A. parryana ssp. deserticum has fruits that are more than double those of A. glandulosa and the round, mostly solid endocarp stones clearly distinguish it from that species.

ACKNOWLEDGMENTS

We thank Nancy James for her early unpublished report of a burl-forming manzanita from Heartbar Peak and Steve Boyd (RSA) for curating these collections.

LITERATURE CITED

ADAMS, J. E. 1940. A systematic study of the genus *Arctostaphylos* Adanson. Journal of the Elisha Mitchell Scientific Society 56:1–62.

KEELEY, J. E., A. MASSIHI, and L. BOYKIN. Phenetic analysis of *Arctostaphylos parryana*. II. Sources of variation. Madroño (in preparation).

WELLS, P. V. 1993. Arctostaphylos. Pp. 545–559 in J. C. Hickman (ed.), The Jepson manual. Higher plants of California. University of California Press, Berkeley.

METASTELMA MEXICANUM (ASCLEPIADACEAE): A NEW COMBINATION AND RE-EVALUATION OF THE STATUS OF BASISTELMA BARTLETT

MARK FISHBEIN¹ and RACHEL LEVIN Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721

Abstract

Intensive collecting in southeastern Sonora, México has clarified the conspecific nature of Cynanchum wigginsii Shinners [Basistelma angustifolium (Torr.) Bartlett] and Basistelma mexicanum (Brandegee) Bartlett. This species is known from apparently disjunct localities in central Sinaloa, southeastern Sonora, and the United States-México border region in Arizona and Sonora. Apparent distributional gaps between these population systems are probably due to insufficient botanical collecting rather than truly disjunct occurrences. The two entities that we treat as a single species were differentiated in the most recent treatment of these taxa by degree of recurvature of the apical anther appendages and the length of the style apex. These differences were based presumably on examination of very few specimens. Our examination of additional collections from a broad geographic area reveals that both characters vary on a local scale and do not covary consistently; thus recognition of two species is unwarranted. Acceptance of Metastelma R. Br. as a genus distinct from Cynanchum L. necessitates the new combination, Metastelma mexicanum (Brandegee) Fishbein & R. Levin. Although separated from *Metastelma* in previous treatments on the basis of the unusual elongate style apex, M. mexicanum is clearly a member of this genus; it possesses the comparatively delicate habit, small cuneate-based leaves, and minute flowers with simple corona scales characteristic of Metastelma.

RESUMEN

Colecciones intensivas del suroeste de Sonora, México han aclarado la esencia conspecífica de Cynanchum wigginsii Shinners [Basistelma angustifolium (Torr.) Bartlett] y Basistelma mexicanum (Brandegee) Bartlett. Esta especie se ha encontrado en localidades aparentemente separadas en Sinaloa central, el suroeste de Sonora, y el area de la frontera entre los Estados Unidos y México en Arizona y Sonora. Estos aparentes vacios distribucionales entre estas poblaciones están probablemente causados por colecciones insuficientes. Las dos especies que presentamos aquí como una especie única se diferenciaban de acuerdo en el estudio más reciente de estas especies por la cantidad de encorvadura de las añadiduras ápicales de las anteras y la longitud del ápice del estilo. Estas diferencias estaban basadas probablemente en el estudio de pocos especímenes. Nuestro estudio de colecciones adicionales de una región más amplia revela que ambos caracteres varían a pequeña escala y no covarían constantemente; por esto el reconocimiento de dos especies no está justificado. La aceptación de Metastelma R. Br. como un género distinto de Cynanchum necesita la combinación nueva, Metastelma mexicanum (Brandegee) Fishbein & R. Levin. Aunque estaba separado de Metastelma en estudios anteriores por el insólito estilo ápice alargado,

¹ Present address: Department of Botany, Washington State University, Pullman, WA 99164-4238.

MADROÑO, Vol. 44, No. 3, pp. 268-276, 1997

M. mexicanum es claramente un miembro de este género; tiene el hábito relativamente delicado, pequeñas hojas cuneadas, y flores diminutas con hojuelas sencillas de la corona que son características de *Metastelma*.

Metastelma R. Br. is a medium-sized genus of probably fewer than 100 species found in both hemispheres of the Americas (Stevens 1985; Liede and Meve 1997). Following Woodson (1941), Metastelma has been treated as part of a very broadly circumscribed Cynanchum L. by some North American workers (e.g., Standley and Williams 1969; Correll and Johnston 1970; Sundell 1981, 1994; Rosatti 1989). This highly inclusive treatment of Cynanchum has not met with general acceptance in North America, and Metastelma has been maintained by several systematists (e.g., Shreve and Wiggins 1964; Wiggins 1980; Stevens 1985, 1988). As noted by Liede and Meve (1997), South American workers have also inconsistently recognized Metastelma. Recently, Liede (1996, 1997a, b; Liede and Meve 1997) has begun to clarify generic circumscriptions within subtribe Metastelmatinae Endl. ex Meisn. (Cynanchinae K. Schum.; Liede 1997b). Although these circumscriptions currently appear to be somewhat provisional, species of Metastelma have stood out as particularly discordant elements within Cynanchum sensu Woodson (Liede and Meve 1997) and the recognition of *Metastelma* appears well founded.

In preparing a treatment of Metastelma for a revised flora of the Río Mayo region of northwestern México (Levin and Fishbein in Martin et al. 1998), we found it necessary to provide a single transfer from Cynanchum to Metastelma. Originally, the specimens in question were identified as Cynanchum wigginsii Shinners (Van Devender et al. 1995). Close study of many herbarium collections of C. wigginsii [=Basistelma angustifolium (Torr.) Bartlett] and the clearly related Basistelma mexicanum (Brandegee) Bartlett (including the types of both species) revealed that the collections from southeastern Sonora were also similar to the type of *B. mexicanum*. The close relationship of specimens assigned to these taxa was first noted by Bartlett (1909), who erected the genus Basistelma to accommodate them as two species. The similarities between the types (and among all collections examined) suggested to us that only a single species was represented. We found that the slight morphological differences in staminal and stylar characteristics noted by Bartlett (1909) and Standley (1924) are variable within small geographic areas (sometimes from the same locality) and that the states of these characters do not covary consistently among herbarium specimens. Thus, we make the following new combination and recognize a new synonym (herbarium acronyms follow Holmgren et al. [1990] and updates).

- Metastelma mexicanum (Brandegee) Fishbein & R. Levin comb. nov.—Melinia mexicana Brandegee, Zoe 5:216. 1905.—Basistelma mexicanum (Brandegee) Bartlett, Proceedings of the American Academy of Arts and Sciences 44:632. 1909.— TYPE: MEXICO, Sinaloa, about 30 mi. east of Culiacan, near Durango border, Cerro Colorado, 1904, T. S. Brandegee s.n. (GH!).
- Metastelma angustifolium Torr., Report on the U.S. and Mexican Boundary Survey 2:159. 1859, non Turcz., Bjulleten' Moskovskogo Občšestva Ispytatelej Prirody. Otdel Biologičeskij 1852: 315. 1852.—Melinia angustifolia (Torr.) A. Gray, Proceedings of the American Academy of Arts and Sciences 12:73. 1877.— Pattalias angustifolius (Torr.) S. Watson, Proceedings of the American Academy of Arts and Sciences 24:60. 1889.—Cynanchum wigginsii Shinners, Sida 1:365. 1964.—TYPE: MEX-ICO, Sonora: Santa Cruz, 1851, C. Wright 1677 (GH, 3 sheets!, US!).

Metastelma mexicanum grows at the upper elevational limit of tropical deciduous forest and in oak-dominated grassland and wood-land in southern Arizona, Sonora, and Sinaloa (Fig. 1). Although it has not yet been collected there, the species is very likely to occur in similar habitats in contiguous southwestern Chihuahua—in the upper watersheds of the Río Yaqui, the Río Mayo, and the Río Fuerte—and perhaps also in northwestern Durango. Like many other members of the genus, it twines on the branches of shrubs and small trees, and upon itself, forming dense tangles under favorable conditions. It is apparently never common; often only a single (occasionally quite robust) individual can be found at any one location (M. Fishbein, personal observation).

Additional specimens examined. MEXICO, Sonora: near Magdalena, 2 Oct 1976, T. R. Van Devender s.n. (ARIZ), Jul 1977, T. R. Van Devender s.n. (ARIZ), 3 Oct 1982, G. Starr 180 (ARIZ, CAS), 14 Aug 1983, T. R. Van Devender s.n. (ARIZ); Rancho Santa Barbara, 3 Jun 1993, P. Jenkins 93-88 (ARIZ, MEXU, MO, UCR, USON); Sierra de Alamos, 19 Aug 1992, V. W. Steinmann s.n. (ARIZ); Sierra Saguaribo, Aug 1935, F. Pennell 19,530 (US), 23 Aug 1993, M. Fishbein 1362 (ARIZ, MO), 24 Aug 1993, M. Fishbein 1448 (ARIZ). UNITED STATES, Arizona: Cochise Co.: Mule Mountains, 19 Sep 1961, L. N. Goodding 299-61 (ARIZ), 302-61 (ARIZ), 14 Oct 1961, L. N. Goodding 439-61 (ARIZ), 5 Sep 1973, T. R. Wentworth 2211 (ARIZ). Santa Cruz Co.: Canelo Hills, Middle Canyon, 19 Sep 1993, M. Fishbein 1500 (ARIZ); Pajarito Mountains, Sycamore Canyon, Sep 1976, J. Kaiser 914 (ARIZ), 13 Aug 1978, L. J. Toolin 20 (ARIZ), 7 Oct 1981, T. R. Van Devender s.n. (ARIZ), 1 Sep 1987, T. R. Van Devender 87-241 (ARIZ); Patagonia

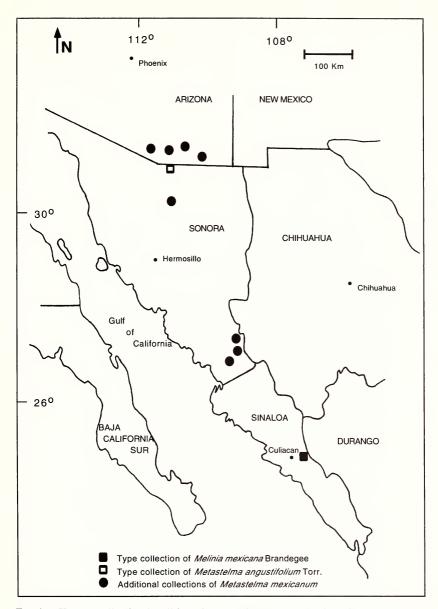


FIG. 1. Known collection localities of *Metastelma mexicanum* in Arizona, U.S., and Sonora and Sinaloa, México. Collection sites within ca. 25 km are represented by a single symbol. Localities of type specimens pertaining to this species are indicated by squares; all other localities are indicated by ovals.

Mountains, 11 Sep 1978, S. P. McLaughlin 1848 (ARIZ); east of Ruby, 19 Nov 1981, T. R. Van Devender s.n. (ARIZ).

Although the earliest epithet applied to this species was *Metastelma angustifolium* Torr., this name was invalid upon publication as a homonym of the slightly earlier *M. angustifolium* Turcz. The earliest validly published basionym pertaining to this species is *Melinia mexicana* Brandegee. (*Melinia* Decne. is now considered to be a relatively distantly related genus in subtribe Oxypetalinae K. Schum. [Liede 1997b].) This species was transferred to *Basistelma* by Bartlett (1909), but has never been assigned to *Metastelma*, necessitating the transfer made here.

Recent treatments of *Metastelma mexicanum* either maintain *Basistelma* as a genus or include *Metastelma* and *Basistelma* in a greatly expanded *Cynanchum*. Kearney and Peebles (1951) recognized *Metastelma* (*M. arizonicum*) and *Basistelma* (*B. angustifolium*) in Arizona. Following Woodson's (1941) concept of an inclusive *Cynanchum*, Shinners (1964) made several transfers from *Metastelma* to *Cynanchum* and also transferred *Basistelma angustifolium* (proposing the nomen novum, *Cynanchum wigginsii*). This generic concept was followed in the most recent treatment of Arizona plants (Sundell 1994). Recently, Liede (1997a, b) assigned taxa referable to *Metastelma mexicanum* to two different genera (see below, "The status of *Metastelma*").

THE STATUS OF BASISTELMA

Basistelma was segregated from Metastelma by Bartlett (1909) and Standley (1924) primarily on the basis of the elongate style apex of the two species here considered to be conspecific. However, this character is found in some individuals of Metastelma arizonicum A. Gray from the Sonoran Desert, and even in other distantly related asclepiadaceous genera, as in Matelea cordifolia (A. Gray) Woodson (M. Fishbein and R. Levin, personal observation). Standley (1924) also contrasted the valvate aestivation of the corolla lobes in bud of Metastelma with the contorted, imbricate aestivation of Basistelma and Cynanchum. However, we have found contorted, imbricate aestivation in some species included in *Metastelma* by Standley (1924), e.g., M. arizonicum A. Gray (as M. watsonianum Standl.), M. barbigerum Scheele, M. palmeri S. Watson, and M. pringlei A. Gray. Thus, the few characteristics previously used to separate Basistelma from Metastelma are inadequate and obscure the close relationship among species of these genera. Recognizing Basistelma would almost certainly create a paraphyletic Metastelma.

THE STATUS OF METASTELMA

Liede (1997a) discussed the circumscription and distinguishing features of *Cynanchum* and related genera that occur in the Amer-

icas. Species of Metastelma are most similar to those of Ditassa R. Br., Orthosia Decne., Tassadia Decne., and Cynanchum sect. Macbridea (Raf.) Liede and sect. Microphyllum Liede. Compared to other sections of Cynanchum and the other genera of Metastelmatinae (Liede 1996, 1997a), these taxa share many characteristics with Metastelma (e.g., delicate twining stems; small, relatively narrow leaves that are never deeply cordate at the base; and minute flowers produced in contracted "umbellate" inflorescence units [sensu Fishbein and Venable 1996]). Distinguishing characteristics of these taxa are conveniently summarized by Liede (1997a, Table 1). The most reliable character to differentiate species of Metastelma from those of similar taxa, as circumscribed by Liede (1997a), is the composition of the corona. Species of Metastelma and Ditassa are distinguished from those of related genera by possessing unfused corona segments located only opposite the stamens; in other similar genera, species possess coronas of fused segments positioned both opposite and alternate the stamens (coronas are absent in some species of Cynanchum sect. Macbridea). Species of these two genera are also the only ones in this group of taxa that possess long, dense, adaxial trichomes of the corolla lobes. Metastelma and Ditassa (which are strictly South American) are distinguished from each other by the adaxial appendage of the corona segments found only in species of Ditassa.

Other characteristics of Metastelma appear to be less reliable for distinguishing these species from those of related genera. Liede (1997a, Liede and Meve 1997) suggested that the presence of the distinctive corolline trichomes noted above is the most reliable distinguishing character of Metastelma. However, we have found only minute corolline trichomes or papillae in several species in North America that we consider to be unambiguous members of Metastelma (e.g., M. cuneatum Brandegee, M. palmeri A. Gray) and species of Ditassa share possession of these trichomes, as noted above (Liede 1997a, Table 1). Liede (1997a, Table 1) also suggested that species of Metastelma can be distinguished from most species of *Cynanchum* by the regular production of two fruits (versus one) per flower; however, this characteristic appears to be exceedingly rare in all species of Metastelma in North America that we have studied, based on examination of plants in the field and numerous herbarium specimens.

Although the species of *Metastelma* are distinguished from those of similar genera by subtle characteristics, we concur with Liede (1997; Liede and Meve 1997) that the distinctive corona morphology merits generic recognition. Although it is possible that a broadly circumscribed *Cynanchum* may be monophyletic with *Metastelma* (and related genera, e.g., *Ditassa*) nested within (essentially Woodson's [1941] position), recent progress in the systematics of *Cynan*-

MADROÑO

chum s.l. suggests the polyphyly of a taxon circumscribed so broadly (Liede 1996). A better case could be made for combining *Metas-telma* and *Ditassa*, but, to our knowledge, this generic concept has not been proposed. Unfortunately, simultaneous phylogenetic study of all relevant taxa has not been attempted as yet. Based on existing evidence, recognition of *Metastelma* is warranted.

Surprisingly, Liede (1997b) treated Basistelma as a synonym of Cynanchum, despite the corona morphology (i.e., unfused segments opposite the stamens) of Metastelma mexicanum, which is diagnostic of Metastelma. However, Liede (1997a) also placed C. wigginsii, inexplicably, in synonymy with Orthosia kunthii Decne. (Cynanchum kunthii [Decne.] Standl., Metastelma angustifolium Turcz.). Species of Orthosia were recognized as distinct from those of Cynanchum by Liede (1997a) based on the apically dentate or toothed, fused corona segments of Orthosia (however, the segments of O. kunthii are untoothed [M. Fishbein, personal observation]). Regardless of the correct generic assignment of O. kunthii, M. mexicanum is clearly not conspecific; specimens that we have identified as O. kunthii (we have not seen the type) possess much smaller corollas with shorter, adaxially glabrous lobes, and corona segments that are fused basally. Specimens of Metastelma mexicanum possess all of the diagnostic features of Metastelma, as noted above, including long, dense adaxial trichomes on the corolla lobes and unfused corona segments opposite the stamens. When identified using Liede's (1997a) key to New World sections of Cynanchum and related genera, they are unambiguously assigned to Metastelma.

INTRASPECIFIC VARIATION IN METASTELMA MEXICANUM

We initially attempted to recognize the southern and northern populations corresponding to Basistelma mexicanum and B. angustifolium of Bartlett (1909) as distinct subspecies of Metastelma mexicanum, but this treatment appears untenable. These entities were distinguished as species by Bartlett (1909) as follows: B. mexicanum was said to differ by possessing a shorter style apex, "more fleshy" corona segments, and more recurved apical anther appendages. However, corona segments appear to be uniformly laminate in all specimens that we have examined. It is noteworthy that Standley (1924) omitted this distinguishing character in his treatment. We have found the other two characters to be variable within populations (i.e., herbarium specimens from the same, precise locality) and to not covary consistently. Long and short style apices are present in both northern and southern populations. Apical anther appendages differ more consistently between northern and southern populations than the length of the style apex: those on plants from Arizona and northern Sonora are typically erect or nearly so, whereas those on

plants from southern Sonora and Sinaloa may be erect, but more commonly have recurved tips. We consider this slight and inconstant distinction insufficient for recognition of infraspecific taxa.

CONCLUSION

Metastelma mexicanum is easily distinguished from other species in the genus in North America, as circumscribed by Liede (1997a). The exceedingly narrow, almost filiform leaves are unlike those of any other species in North America, and the elongate style apex is shared only with some plants of *M. arizonicum*. The combination of these two characteristics, in addition to the unique, erect, apical anther appendages, serves to distinguish *M. mexicanum* from other species of *Metastelma* in North America.

Metastelma mexicanum is as yet a poorly known species. We examined all specimens collected in México housed at the cited herbaria and all specimens collected in Arizona housed at ARIZ. The species appears to rare throughout its range (Fishbein and Warren 1994; Levin and Fishbein in Martin et al. 1998). Further collecting on the Pacific slope of the northern Sierra Madre and in the mountains of northeastern Sonora is required to definitively evaluate previously hypothesized patterns of morphological variation within this species. Proposed relationships between *M. mexicanum* and other species of *Metastelma* would be highly speculative at this time. The genus is badly in need of both monographic and phylogenetic study.

ACKNOWLEDGMENTS

We are grateful to John Reeder for nomenclatural advice. We thank the staff at ARIZ for the handling of loan material and the curators of GH and US for prompt transmittal of loan specimens. We are also very grateful to Shelley McMahon for assistance with the preparation of Figure 1 and Henar Alonso-Pimentel for critically reviewing the use of Spanish. Comments and suggestions from Phil Jenkins and three anonymous reviewers improved this paper.

LITERATURE CITED

- BARTLETT, H. H. 1909. Descriptions of Mexican phanerogams. Proceedings of the American Academy of Arts and Sciences 44:630–637.
- CORRELL, D. S. and M. C. JOHNSTON. 1970. Manual of the vascular plants of Texas. Texas Research Foundation, Renner, TX.
- FISHBEIN, M. and D. L. VENABLE. 1996. Evolution of inflorescence design: theory and data. Evolution 50:2165–2177.

— and P. WARREN. 1994. Population studies of sensitive plants of the Lone Mountain Ecosystem Management Area, Coronado National Forest, Arizona. Unpublished report to the Arizona Field Office of The Nature Conservancy and Coronado National Forest.

HOLMGREN, P. K., N. H. HOLMGREN, and L. C. BARNETT. 1990. Index herbariorum, 8th ed., pt. 1. New York Botanical Garden, New York.

- KEARNEY, T. H. and R. H. PEEBLES. 1951. Arizona flora. University of California, Berkeley.
- LIEDE, S. 1996. Cynanchum-Rhodostegiella-Vincetoxicum-Tylophora (Asclepiadaceae): new considerations on an old problem. Taxon 45:193–211.
 - ——. 1997a. American Cynanchum (Asclepiadaceae)–A preliminary infrageneric classification. Novon 7:172–181.
 - —. 1997b. Subtribes and genera of the Asclepiadeae (Apocynaceae, Asclepiadoideae)—a synopsis. Taxon 46:233–247.
 - and U. MEVE. 1997. Some clarifications, new species, and new combinations in American Cynanchinae (Asclepiadaceae). Novon 7:38–45.
- MARTIN, P. S., D. YETMAN, M. FISHBEIN, P. JENKINS, T. R. VAN DEVENDER, and R. WILSON. 1998. Gentry's Río Mayo Plants. University of Arizona, Tucson.
- ROSATTI, T. J. 1989. The genera of suborder Apocyninae (Apocynaceae and Asclepiadaceae) in the southeastern United States. Asclepiadaceae. Journal of the Arnold Arboretum 70:443–514.
- SHINNERS, L. 1964. Texas Asclepiadaceae other than Asclepias. Sida 1:358-367.
- SHREVE, F. and I. WIGGINS. 1964. Vegetation and flora of the Sonoran Desert. Stanford University Press, Stanford, CA.
- STANDLEY, P. C. 1924. Trees and shrubs of Mexico. Asclepiadaceae. Contributions from the United States National Herbarium 23:1166–1194.
 - —— and L. O. WILLIAMS. 1969. Asclepiadaceae. *In* Flora of Guatemala. Fieldiana, Botany 24(8):407–472.
- STEVENS, W. D. 1985. Asclepiadaceae. Pp. 228–241 *in* J. Rzedowski and G. C. de Rzedowski (eds.), Flora Fanerogámica del Valle de México. Escuela Nacional de Ciencias Biológicas, Instituto de Ecología, México, D.F.
 - ———. 1988. New names and combinations in Apocynaceae, Asclepiadoideae. Phytologia 64:333–335.
- SUNDELL, E. 1981. The New-World species of *Cynanchum* subgenus *Mellichampia* (Asclepiadaceae). Evolutionary Monographs 5:1–62.
- ———. 1994. Asclepiadaceae (treatment for Vascular Plants of Arizona). Arizona-Nevada Academy of Science 27:169–187.
- VAN DEVENDER, T. R., V. W. STEINMANN, J. F. WIENS, and C. D. BERTELSEN. 1995. Noteworthy collections. *Cynanchum wigginsii* in Sonora. Madroño 42:410.
- WIGGINS, I. 1980. Flora of Baja California. Stanford University, Stanford, CA.
- WOODSON, R. E., JR. 1941. The North American Asclepiadaceae. Annals of the Missouri Botanical Garden 28:193–244.

ATRIPLEX PACHYPODA (CHENOPODIACEAE), A NEW SPECIES FROM SOUTHWESTERN COLORADO AND NORTHWESTERN NEW MEXICO

HOWARD C. STUTZ Department of Botany and Range Science, Brigham Young University, Provo, UT 84602

GE-LIN CHU Institute of Botany, Northwest Normal University, Lanzhou, Gansu, China 730070

ABSTRACT

Atriplex pachypoda is a newly described annual species from southwestern Colorado and northwestern New Mexico. It occurs in alkaline seepage areas and adjacent disturbed slopes in La Plata county, Colorado, and Rio Arriba county, New Mexico. It is morphologically most similar to *A. caput-medusae* Eastwood, but differs in its smaller, more spreading habit, narrow-ovate to ovate-elliptical instead of deltoid-ovate leaves, flattened instead of uncompressed fruiting-bracts, small, cone-shaped, instead of large, flattened, fruiting-bract appendages, larger, central, marginal tooth of fruiting-bract, more stout fruiting-bract pedicel, and later flowering- and fruiting-periods.

This somewhat obscure annual species was first found 14 Aug 1991 at the south edge of Dulce, Rio Arriba County, New Mexico. Only two other populations have been found, one at the southwest edge of Bayfield, La Plata County, Colorado, the other in Dry Creek, north of highway 140, about 7 km west of Bayfield.

Atriplex pachypoda Stutz & Chu, sp. nov. (Fig. 1)—TYPE: USA, Colorado, La Plata Co., Dry Creek, ca. 7 km W of Bayfield, T34N R7W S12, 21 Sep 1995, H. C. Stutz 9822 (holotype, BRY).

Herba annua, 10–20 cm alta. Caulis erectus, ramosus; basales rami oblique ascendentes vel decumbentes, fere centrale caule aequilongi, tetragoni vel fere sic, plerumque leviter purpureorubelli, sparse furfuracei. Folia Kranz-typorum anatomiis, petiolata; lamina angusti-ovata, usque ovato-elliptica, 1–1.5 cm longa, 0.5–1 cm lata, apice obtusa vel breviter acuminata, basi cuneata, margine integra, costa conspicua, utrinque dense furfuracea, cinereo-viridis; petiolus 2–5 mm longas. Staminates et pistillati flores mixti in glomerulos, axillares ad totos ramos; perianthium staminalis floris globosum, ca. 1 mm diam. 4–5-partium; segmenta elliptica, apice leviter cucullata, membranacea, secus costam leviter carnosa et viridia; stamina 4–5, antheris ca. 0.3 mm longis, filamentis filiformibus ca. 0.5 mm longis. Fructiferae bracteae transverso-oblongae, compressae, 4–5 mm lon-

MADROÑO, Vol. 44, No. 3, pp. 277-281, 1997

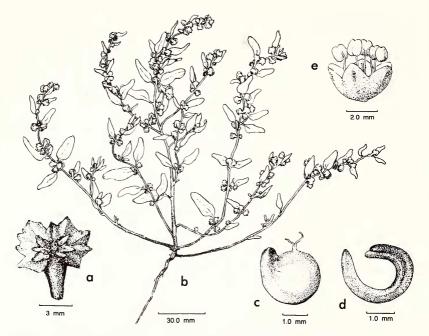


FIG. 1. *Atriplex pachypoda.* a. Fruiting bract. b. Habit. c. Utricle. d. Embryo. e. Male flower. (Drawings by Marcus Vincent).

gae, 4–5 mm latae, margine irregularter serratae, medio dente quam 2 contigui laterales dentes flerumque leviter minori, utrinque saepe aliquot irregulibus cornicutatis appendicibus; stipes fructiferae bracteae validus, 2–3.5 mm longus, 1–2 mm diam. Utriculus ovatus, membranceo pericarpio. Semen flavo-brunnolum, ca. 2 mm latum, perispermio farinaceo; radicula supera. Chromosotum numerus 2n=18.

Proxima Atriplex caput-medusae Eastwood, quae differt folius deltato-ovatus usque rhomboideo-ovalis; fructiferis bracteis margine partitis.

Annual herb, 10–20 cm tall. Stem ascending, much branched, basal branches oblique, mostly decumbent, nearly as long as central stem, tetragonous or nearly so, usually slightly purple-reddish, sparsely furfuraceous. Leaves petiolate, petiole 2–5 mm long; blades narrow-ovate to ovate-elliptical, 1-1.5 cm long, 0.5–1 cm wide, apex obtuse or acuminate, base cuneate, entire, midrib conspicuous, densely furfuraceous on both surfaces, grey-green in color; Kranz-type anatomy. Male and female flowers in mixed glomerules, axillary throughout all branches; perianth of staminate flower depressed, globose, ca. 1 mm in diam., 4–5-parted; segments elliptical, slightly

hooded at apex, membranaceous, midrib slightly fleshy, green; stamens as many as perianth segments, anthers ca. 0.3 mm long, filaments ca. 0.5 mm long; rudimentary pistil present, punctiform. Fruiting bracts transverse-oblong in outline, 3.5-4 mm long, 4-5mm wide, depressed, with stout, short stalk; margins irregularly denticulate, each marginal tooth with prominent vein to apex, middle tooth equal to, or slightly smaller than 2 contiguous teeth; usually with several irregular cone-shaped appendages on each surface; stalk of fruiting bracts 2–3.5 mm long, 1–2 mm wide. Utricle ovate, with membranaceous pericarp. Seed yellow-brown, ca. 2 mm broad; perisperm farinaceous; radicle superior. Flowering and fruiting period: August–October. Chromosome number: 2n=18 (determined from aceto-carmine squashes of pollen mother-cells derived from anthers of staminate flowers fixed and stored in 5% acetic acid).

Paratypes. USA, Colorado: La Plata Co., Bayfield, T34N R7W S10, 3 Sep 1992, *H. C. Stutz 95696* (BRY); Bayfield, 17 Sep 1993, *H. C. Stutz 95937* (BRY); Dry Creek, 4 mi W of Bayfield, T34N R7W S12, 2 Oct 1993, *H. C. Stutz 95954* (BRY); SW side of Bayfield, 19 Oct 1993, *H. C. Stutz 95970* (BRY); Bayfield, 18 Aug 1994, *H. C. Stutz 9663* (BRY); Dry Creek, 15 mi E of Durango, 16 Aug 1995, *H. C. Stutz 9806* (BRY). New Mexico: Rio Arriba Co., Dulce, S edge of town, T31N R2W S35, abundant, 14 Aug 1991, *H. C. Stutz 95586* (BRY); Dulce, S edge of town, scarce, 8 Sep 1994, *H. C. Stutz 9667* (BRY).

Taxonomic relationships. Atriplex pachypoda appears to be most closely related to A. caput-medusae but differs in several significant characteristics including smaller stature (10-20 cm vs. 20-30 cm), narrow-ovate to ovate-elliptical leaves (5-10 mm wide, 10-15 mm long), instead of rhomboid-ovate to deltoid-ovate leaves (15-20 mm wide, 10-25 mm long) (Fig. 2) and flattened instead of uncompressed fruiting-bracts (Fig. 2). Fruiting-bracts of A. pachypoda have dentate margins and a few lateral cone-shaped appendages, whereas fuiting-bracts of A. caput-medusae have irregularly parted margins and bear numerous lateral, flattened appendages (Fig. 2). The central marginal tooth of A. pachypoda is nearly as large as the contiguous marginal teeth whereas, in A. caput-medusae, the central tooth is minute and obscured by much larger contiguous teeth. Both A. pachypoda and A. caput-medusae have fruits with conspicuous pedicels, but pedicels of A. caput-medusae are elongate (5-6 mm) and narrow, tapering from ca. ¹/₂ mm to ca. 1 mm in diameter whereas those of A. pachypoda are shorter (2-4 mm), and more massive, tapering from ca. 1.5 mm to ca. 2.0 mm (Fig. 2). Anthesis in A. caput-medusae is in early spring (May-June); anthesis in A. pachypoda is in late summer (August-October). Both A. pachypoda and A. caput-medusae are diploids (2n=18) (determined from aceto-car-

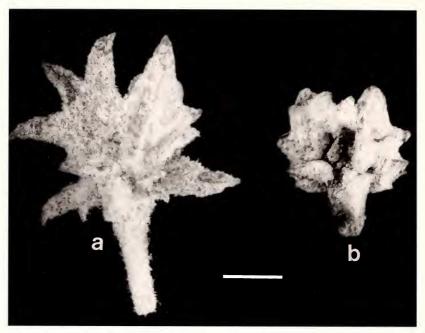


FIG. 2. Fruiting bracts of *Atriplex caput-medusae* (left) and *A. pachypoda* (right). Bar = 3 mm.

mine squashes of pollen-mother-cells taken from anthers fixed and stored in 5% acetic acid).

Distribution and habitat. Atriplex pachypoda has been found in only three localities: southwest side of Bayfield, LaPlata county, Colorado, along Dry Creek, about 7 km west of Bayfield, and at the south outskirts of Dulce, Rio Arriba county, New Mexico. Several intensive searches have been made throughout southwestern Colorado and northwestern New Mexico but no other populations have yet been found. However, because plants were abundant in the population at Dulce, New Mexico, in 1991 but scarce or absent in 1993 and were sometimes abundant and at other times scarce, at Bayfield, Colorado, other populations may yet be found when climatic conditions are favorable for their growth.

The three known populations of *A. pachypoda* are in raised areas near alkaline seepage areas. No *A. pachypoda* plants were found in the wet bottoms of these seepage areas but were plentiful on slightly elevated terrain within the seepages, and on the shoulders of nearby roadcuts.

Associated species. Atriplex pachypoda sometimes occurs in small, pure stands usually covering areas of less than 5.0 m^2 with

no other associated species but is often accompanied by plants of *Atriplex powelli* Watson, *A. subspicata* Rydberg, *A. heterosperma* Bunge, *Chrysothamnus nauseosus* (Pallas) Britt, *Distichlis spicata* (L.) Greene and *Polygonum* sp.

Phenology. Flowering and fruiting is mostly in late summer (August–October). Plants of *A. pachypoda* and *A. caput-medusae* grown in greenhouses and nurseries at Brigham Young University, Provo, Utah, from seed collected from plants growing in natural populations showed the same distinctive attributes expressed by plants growing in nature, indicating high heritability of these characteristics.

ACKNOWLEDGMENTS

We thank BHP-Minerals and Brigham Young University for financial assistance, and the curators of the following herbaria for loans of specimens and access to their collections: BRY, CAS, GH, NY, RM, RSA, UC, UNM, and US.

NOTEWORTHY COLLECTIONS

BRITISH COLUMBIA

SILENE SPALDINGII Wats. (CARYOPHYLLACEAE).—Tobacco Plains, vicinity of Roosville, between Davis Rd. and the Canada-U.S. border on Beau West Ranch, UTM 6412 54296, elev 850 m, on disturbed grassland with Lupinus sericeus, Hypericum perforatum, Castilleja tenuis, and Castilleja thompsonii, 8 Aug 1995, Michael T. Miller, verified by G. A. Allen (UVIC).

Previous knowledge. This rare campion is known from about 70 localities in Washington, Oregon, Idaho and Montana (B. Heidel, personal communication). The newly reported population (with an estimated minimum size of 100 plants) is 0.6 km N of the U.S. border, and approximately 1.3 km NE of the nearest documented occurrence in Flathead Co., Montana. We thank George Douglas of the B.C. Conservation Data Centre and Bonnie Heidel of the Montana Natural Heritage Program for providing us with information on known and suspected occurrences of this species along the B.C.-Montana border.

Significance. First record for Canada, and the most northerly record for this species. It is not clear whether the new record is the result of recent colonization, or has been overlooked by previous collectors. The locality is approximately 7 km N of the Dancing Prairie preserve in Montana, which harbors probably the largest known population of *S. spaldingii*.

---MICHAEL T. MILLER and GERALDINE A. ALLEN, Department of Biology, University of Victoria, Victoria, British Columbia V8W 3N5, Canada.

A REVISION OF THE GENUS HESPERALOE (AGAVACEAE)

GREG STARR Starr Nursery, 3340 W. Ruthann Rd., Tucson, AZ 85745

Abstract

Hesperaloe is a North American genus consisting of three described species. Recent exploration of northern Mexico for plants with horticultural possibilities has resulted in the discovery of three new taxa. These are geographically isolated from each other and from the three previously described taxa. Descriptions and illustrations for two new species and one new subspecies are provided. A key to all five species is included.

RESUMEN

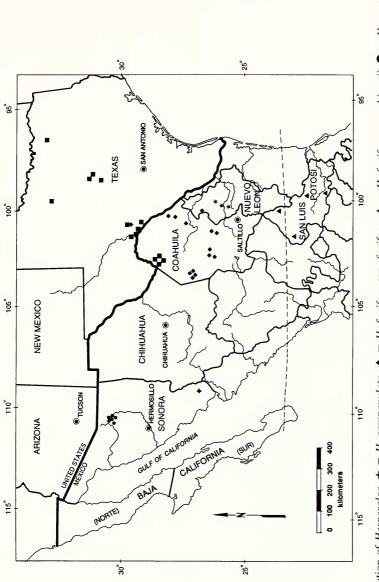
Hesperaloe es un género norteamericano que consiste en tres especies ya anteriormente descritas. Recientemente se han descubierto tres nuevas taxa en México norteño en exploraciones para plantas con posibilidades hortícolas. Las nuevas taxa están aisladas geográficamente la una de las otras y de las tres descritas anteriormente. Se encuentran aquí descripciones e ilustraciones de las dos nuevas especies y la nueva subspecie. También se incluye una clave de las cinco especies.

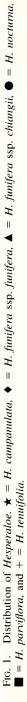
INTRODUCTION

Hesperaloe is a North American genus consisting of six taxa. Four taxa occur on the eastern side of the Sierra Madre Occidental, from Texas to San Luis Potosí, Mexico, while the other two taxa occur on the western side of the Sierra Madre Occidental, in Sonora, Mexico (Fig. 1). The genus was erected by Engelmann in 1871 to accommodate the recently described *Aloe yuccaefolia* A. Gray. However, Torrey (1859) had previously described *Yucca parviflora* which, according to Coulter (1894) included the taxon then known as *Hesperaloe yuccaefolia* Engelmann. The combination became *Hesperaloe parviflora*. (Torrey) Coulter.

In 1862, Koch described Yucca funifera which Trelease (1902) decided fit better in Hesperaloe and made the combination Hesperaloe funifera (Koch) Trelease. It was not until 1967 that another species of Hesperaloe was discovered, when Gentry (1967) described Hesperaloe nocturna from Sonora. Although flowers of H. funifera and H. nocturna are similar, plants are distinct vegetatively, separated geographically by about 750 km, and occur on opposite sides of the Sierra Madre Occidental. Engard (personal communication) proposed the name Hesperaloe chiangii for plants growing in San Luis Potosí. His life was cut short before he could continue his proposed work on the genus. After examining a specimen growing in his yard, I pursued this taxonomic question. Prior to my ar-

MADROÑO, Vol. 44, No. 3, pp. 282-296, 1997





ranging a collecting trip to San Luis Potosí, two other undescribed taxa were found in two widely separated localities, one occurring in central Nuevo León, Mexico, the other in southern Sonora, Mexico. In light of these developments, it became apparent that a revision of the genus *Hesperaloe* was needed. The present revision is based on field and horticultural work with all taxa.

Systematic Treatment

HESPERALOE: Engelmann in King, Geological Exploration of the 40th Parallel. 5:497. 1871.

Short- to long-rhizomatous perennials with stemless rosettes of leaves either tightly packed or widely separated and forming large rings. Main roots thick and fleshy, with many fibrous feeder roots. Leaves few to many, either thin, narrow, and arching to recurved or thick, broad, and stiffly erect, canaliculate; margins brown or white; marginal fibers thin and tightly curled to thick and nearly straight, white or gray. Flowering stalk terminal from the center of mature rosettes, ascending, to 4 m tall, racemose or paniculate with 3–8 lateral side branches in the upper one-half. Flowers on indeterminate lateral spurs, either on main stalk or side branches. Flower color combination of green, white, and purplish-brown to red, pink, salmon, or coral to rarely yellow. Corolla shape tubular to narrowly to broadly campanulate or rotate-campanulate. Stamens included to exserted. Fruit a woody, dehiscent capsule, beaked or not, transversely rugose, persistent. Seeds large, black, flat, and thin.

KEY TO THE SPECIES

- 1. Tepals white with greenish purple midstripe, reflexed at anthesis.

1' Tepals pink, red, or coral, reflexed or straight, forming a tube.

- 4. Leaves thin and flexible, spreading, 0.5–1.0 m long, maximum width 5–8 mm wide; flowers rotate; tepals pinkish-red, reflexed, to 13 mm long; fruits globose, beakless or with a beak ≤1 mm long. 5. H. tenuifolia
- 4' Leaves stiff, upright to spreading, more than 8 mm wide; flowers tubular to campanulate; tepals longer than 15 mm; fruits with beak >4 mm long.
 - 5. Leaves dark green, recurved and twisting, deeply canaliculate, 30–60(120) cm long, less than 15 mm wide; flowers tubular; seeds 9–10 mm long, 6–7 mm wide 4. *H. parviflora*
 - 5' Leaves medium green, erect to spreading, not deeply canaliculate;

60–105 cm long, 15–26 mm wide flowers tubular-campanulate to campanulate; seeds 6–9 mm long, 5–6 mm wide. 1. *H. campanulata*

 Hesperaloe campanulata G. D. Starr, sp. nov. (Fig. 2)—TYPE: USA, Arizona: (MEXICO, Nuevo León 550 m, 26°13'N, 100°7'30"W) Grown in author's garden in Tucson from an offset collected 11 Nov 1989 at Mamulique micro-ondas; *Starr 93-001* (holotype: ARIZ!; isotypes: TEX!, MO!, MEXU!).

Planta acaulis, cespitosa, 0.6–1 m lata; foliis lineareo-lanceolatus, 60–105 cm longis, 1.5–1.6 cm latis, margine angusto sparse filifero; inflorescentia simplici paniculata, 3 metralis; flores pedicillati, tepala roseus margine albus 18–22 mm longa, 4–8 mm lata; capsulae globosae 2–3 cm longae, 2–2.5 cm latae; semina nigra 6–9 mm longa, 5–6 mm lata.

Plants acaulescent, forming moderately caespitose clumps to 0.6–1 m across. Leaves stiff and erect to slightly spreading, canaliculate, linear-lanceolate, 60–105 cm long, 15–26 mm wide at widest point (one-third from base) tapering to tip, medium green, margins finely filiferous. Inflorescence 3 m long, raceme or panicle with 2–5 branches in upper one-third. Flowers tubular-campanulate to broadly campanulate; pedicels 8–13 mm long; outer tepals linear to linear-lanceolate, adaxial face white, abaxial face pink with broad, white margins, 18–22 mm long, 4–8 mm wide; stamens and pistill included; filaments 14–15 mm long, adnate to tepal base for 3 mm; anther sacs 3 mm long: ovary 6 mm long, 4 mm wide at anthesis, style 9–13 mm long. Capsules globose or oblong, 2–3 cm long (excluding beak) 2–2.5 cm wide, beak 4–11 mm long; seeds black, 6–9 mm long, 5–6 mm wide.

Paratypes. MEXICO, Nuevo León; 13 miles N of Sabinas Hidalgo, Mexico highway 85, 400 m, 26°38'N, 100°01'W 15 Aug 1990 *Starr 90-001* (ARIZ); 35 miles N of Sabinas Hidalgo on Mexico highway 85, 100 m, 26°52'N, 99°49'30"W, 16 May 1991, *Starr 91-001* (ARIZ).

Phenology and distribution (Fig. 1). Flower spikes begin to appear in late March or early April with flowering extending into October. Flowers open in the evening and are pollinated during the night by bats and hawkmoths. The following day, flowers close some, forming a tube and are visited by hummingbirds. Hesperaloe campanulata occurs in open Chihuahuan Desert scrub on limestone slopes and hillsides. Associated species include Acacia berlandieri, Acacia farnesiana, Acacia rigidula, Bauhinia lunarioides, Cassia greggii, Cercidium texanum, Cordia boissieri, Fraxinus greggii, Guaiacum angustifolium, Leucophyllum frutescens, Vauquelinia angustifolia var. heterodon, and Yucca rostrata. The species is known

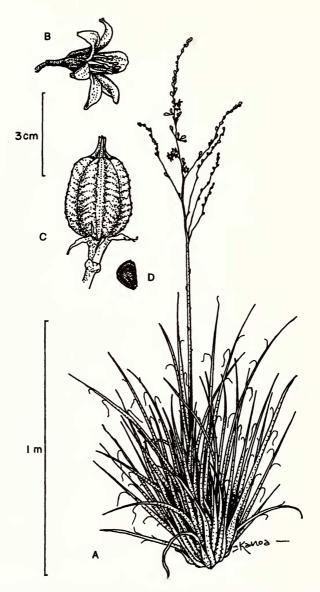


FIG. 2. Hesperaloe campanulata. A. Habit. B. Flower. C. Capsule. D. Seed.

only from a limited area in north-central Nuevo León at 500–600 m. Annual precipitation in this limited geographical range varies from 500 to 700 mm.

Hesperaloe funifera (Koch) Trelease, Annual Report of the Missouri Botanical Garden 13:36. 1902.—Yucca funifera Koch, Belgique Horticole 12:132, 1862.—Agave funifera Lemaire, L'Illustration Horticole. 11(misc.): 65. 1864.—Yucca funifera Lemaire, L'Illustration Horticole. 13:99. 1866.—TYPE: None cited. NEOTYPE (here designated): MEXICO, Coahuila; 4 miles east of Esmeralda Mine along road to Cuatro Cienegas, 8 May 1973, R. G. Engard and H. S. Gentry 23241 (neotype: ARIZ!).

Hesperaloe davyi Baker, Kew Bulletin of Miscellaneous Information 1898:226.—TYPE: (probably a specimen preserved in K; Baker cited source as plant grown in botanical garden of University of California, Berkeley and sent by J. Burtt Davy. (Isotype: UC!)

Plants caespitose, forming clumps up to 1.5 m across, or long rhizomatous and forming fairy rings to 2 m or more in diameter. Leaves stiff and erect, light to dark green or yellowish-green, canaliculate, linear-lanceolate or lanceolate, 1-2 m long, 3-6 cm wide, margins brown, medium to coarsely filiferous with white or gray loosely coiled fibers. Inflorescence a 2-4 m tall panicle with 3-8 branches mostly in upper one-half of stalk. Flowers rotate-campanulate, in indeterminate fascicles; tepals white on adaxial face, 17-20 mm long, abaxial face of inner tepals green and white with a narrow center stripe tinged brownish purple, 8-9 mm wide, abaxial face of outer tepals green at base and reddish purple on upper twothirds, 6-7 mm wide; stamens and pistil included; ovary at anthesis 10-12 mm long and 4-5 mm wide; pedicel 5-6 mm long. Capsules globose or broadly oblong, 2.5-3.5 cm long 2.5-3.5 cm wide, sharply beaked, beak 2–4 mm long; seeds 8–9 mm long, 5–7 mm wide, black.

In 1862, Koch gave a minimal description of *Yucca funifera* from material given to him by Jean Verschaffelt, a collector of plants for horticulture. There was no type designated and there are no known existing specimens that were used by Koch. Lemaire (1864), without mentioning either Koch or Verschaffelt, described *Agave funifera* from material introduced from Mexico by the Tonel Brothers. Again there was no type specimen designated and there are no known existing specimens. Then in 1866, Lemaire in his treatise on *Yucca* wrote that he mislaid the documents concerning this species, and proceeded to give a brief description of *Yucca funifera*. Apparently Lemaire changed his mind on the correct placement of the species, but still did not designate a type specimen. *Hesperaloe davyi* was named by Baker (1898) from material sent to him by Davy. Baker stated that the material he received from Davy was from the garden

at the University of California at Berkeley. Although he did not designate a type, Baker's description fits that of Hesperaloe funifera. In 1902, Trelease mentioned that Davy told him (Trelease) that there was no record of the source of the seeds from which the plant Baker used for his description was grown. However, he went on to say that Franceschi of Santa Barbara stated that two original plants were raised, with one flowering in 1898, providing the material for which Baker based his description. Franceschi sent suckers from the other plant to Kew and to the Missouri Botanical Garden. Trelease (1902) listed Hesperaloe engelmannii Baillon and H. engelmannii Urbina as synonyms for *H. funifera*. However, the references are simply catalog listings and were not nomenclatural acts by either author. Both references are based on Pringle's number 3911 from Hacienda de la Angostura which was originally misidentified. Hesperaloe engelmannii was a name used by Krauskopf for plants he collected along the western branch of the Nueces River. Krauskopf described these as having reddish petals that is indicative of Hesperaloe parviflora, not H. funifera. Therefore, the references to Hesperaloe engelmannii as a synonym of Hesperaloe funifera are incorrect. Trelease (1902) was the first to make reference to an actual specimen that was collected and deposited in a herbarium. He stated that the Engelmann herbarium (now at MO) contained a specimen collected by Wislizenus in 1847 at Cerralvo northeast of Monterey. He also mentioned capsules collected by Parry in 1878 from "the plains between Monterey and the Rio Grande" as being similar to those collected by Wislizenus. Trelease (1902) mentioned a third specimen that was collected by Wood in 1900 in the state of Nuevo León that is in the herbarium of the Field Columbian Museum. None of these three specimens represent type material and a neotype is hereby designated.

2a. Hesperaloe funifera (Koch) Trelease subsp. funifera.

Plants caespitose, forming clumps up to 1.5 m across. Leaves stiff, erect, light green or yellowish-green, canaliculate, linear-lanceolate or lanceolate, 1–2 m long, 3–4 cm wide (when flattened) from base to middle, tapering from middle to apex, margins brown, with 1 mm thick, white or gray loosely coiled fibers.

Phenology and distribution (Fig. 1). Inflorescences begin showing in spring with flowers appearing from April through August or September. This subspecies occurs in central and northeastern Coahuila and one locality in western Nuevo León at elevations of 500–1000 m. Average annual precipitation ranges from 100 to nearly 500 mm. Associated plants include Acacia rigidula, Agave lechuguilla, Cordia boissieri, Larrea divaricata, Leucophyllum frutescens, Opuntia leptocaulis, and Prosopis glandulosa. There is an unusual population that occurs within a five mile stretch along Nuevo León Highway 1. All plants have leaves about 1 m long. Some plants have typical *H. funifera* flowers while others have flowers more campanulate-rotate with tepals flushed pinkish-red along the margin.

Specimens examined. MEXICO, Coahuila; 23 miles SW of Allende, 1 May 1959, D. S. Correll and I. M. Johnston 21277 (LL); Peyotes (Kilometer 88), 27 Apr 1900. Trelease (MO); 63 miles S of Piedras Negras on Mexico Highway 57, 17 Aug 1971, L. McGill, B. Parfitt, and D. Keil 7841 (ARIZ); on desert near Rancho Santa Teresa S of Castaños, 19 Jun 1936, F. L. Wynd and C. H. Mueller 187 (ARIZ); 11–12 miles SW of Cuatro Cienegas on road to San Pedro, 15 Oct 1972, R. G. Engard and H. S. Gentry 23138 (ARIZ); 2.5 miles E of Esmeralda on road to Est. del Oro, N of Sierra Mojada, 27°16'N, 103°38'W, 20 Sep 1972, J. Henrickson 7830 (ARIZ); 3–4 miles N of San Lazarus on highway to Monclova, 9 Oct 1972, R. G. Engard and H. S. Gentry 23108 (ARIZ). Nuevo León; Rancho Resendez, Lampazos, 24 Jun 1937, M. T. Edwards 341 (ARIZ); 3.9 miles S of Lampazos on Mexico Highway 1, 15 Aug 1990, G. Starr s.n. (ARIZ).

2b. Hesperaloe funifera (Koch) Trel. subsp. chiangii G. D. Starr subsp. nov. (Fig. 3)—TYPE: MEXICO, San Luis Potosí; km 144 on Mexico highway 57 between Matehuala and San Luis Potosí to the west of the pueblito of Pozos Santa Clara, in grasslands with Agave scabra, Cassia wislizenii, Koeberlinia spinosa, Larrea divaricata, Prosopis laevigata, and Yucca australis, 23°15'N, 100°33'W, 1500 m, E. Garcia Moya s.n. (holotype: DES!).

Subspecies haec ab *H. funifera* ssp. *funifera* differt planta rhizomatosus longissimus, foliis 6 cm latis, marginalis fibris incrassatus ad 2–3 mm.

Plants acaulescent, long rhizomatous, forming wide clumps or fairy rings to 2 m or more in diameter. Leaves stiff, erect, medium to dark green, deeply canaliculate, lanceolate, reaching 1.5 m long, 5–6 cm wide (when flattened) from the base to the middle, tapering from the middle to the apex, the marginal fibers coarse, 2–3 mm diameter, white to gray near point of attachment, straight to slightly coiled.

Phenology and distribution (Fig. 1). Flowering period for ssp. *chiangii* is currently unknown. When three populations were visited in August 1990 only the population near Santo Domingo, San Luis Potosí, showed evidence of flowering that year. Flower stalks with ripe capsules were present and seed was collected. *Hesperaloe funifera* ssp. *chiangii* is geographically separated from ssp. *funifera*. The subspecies *chiangii* is locally common on flats and open slopes

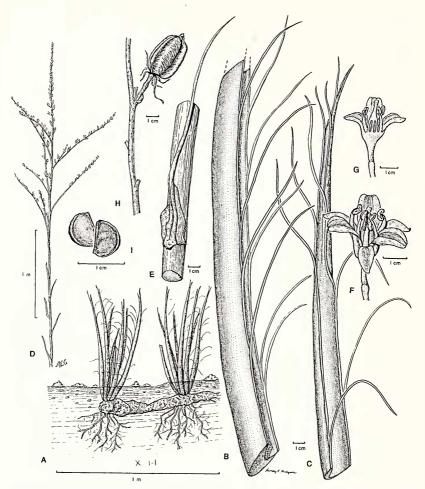


FIG. 3. *Hesperaloe funifera* ssp. *chiangii*. A. Habit. B. Leaf lower 1/5th. C. Leaf upper 1/5th. D. Inflorescence. E. Inflorescence showing bract. F. Flower. G. Flower cross section. H. Portion of infructescence with capsule. I. Seed.

in San Luis Potosí. Average annual precipitation ranges from 300–600 mm. Associated plants include Acacia spp., Agave spp., Fouquieria splendens, Prosopis laevigata, and Yucca filifera.

Paratypes. MEXICO. San Luis Potosí: Hacienda de Angostura, 5 Aug 1891, Pringle 3911 (UC, MO, NY, F, MICH); 12 miles NW of Cd. del Mais along highway to Cd. San Luis Potosí, 19 February 1951, E. C. Ogden, C. L. Gilly, and E. Hernandez. 51119 (ARIZ); km 570 carretera Mexico-Piedras Negras, 18 May 1957, Rzedowski 8709 (TEX); near Santo Domingo, Hwy 80, 26–28 January 1952, H. S. Gentry 11512 (ARIZ).

 Hesperaloe nocturna H. S. Gentry, Madroño 19:74–78. 1967.— TYPE: MEXICO, Sonora; 15 miles SE of Magdalena along road to Cucurpe, by Sierra Baviso, 3,200–3,500 feet, 21 May 1963, *Gentry and Felger 19988* (holotype: US!).

Plants densely caespitose, forming clumps to 1–2 m across. Leaves upright and arching, linear, 1–1.5 m long, 1–2 cm wide at base, long attenuate at apex; margins narrow, brown, finely filiferous with white, irregularly wavy fibers. Inflorescence a slender panicle to 1.5–4 m high, with 2–3 branches in upper one-half. Flowers nocturnal, campanulate-rotate, in indeterminate fascicles; tepals greenish-white on adaxial face 15–25 nm long, abaxial face of inner tepals with broad, reddish-purple center stripe, 8–9 mm wide, abaxial face of outer tepals reddish with greenish-brown center stripe, 6–7 mm wide; stamens and pistil included; filaments attached to base of tepals for 3 mm; ovary at anthesis 10 mm long and 4 mm wide; pedicels 14–16 mm long. Capsules depressed ovoid or oblong, 3–4 cm long, 2.5–4.5 cm wide, short beaked; seeds black, 11 mm long, 8 mm wide.

Phenology and distribution (Fig. 1). Flowering occurs from Apr to Jul, with seed set coinciding with summer rains. Known only from north-central Sonora at 950–1150 m elevation with Acacia occidentalis, Acacia greggii, Berberis haematocarpa, Cercidium floridum, Coursetia microphylla, Fouquieria splendens, Prosopis velutina, and Yucca arizonica. Also reported from one sterile specimen in northeastern Sonora where it was growing on a steep canyon wall with Ficus petiolaris, Justicia candicans, and Quercus sp.

Specimens examined. MEXICO. Sonora. 20.4 miles SE of Magdalena on Cucurpe road, 11 Apr 1976, T. R. Van Devender, K. B. Moodie, and S. F. Hale (ARIZ); Rancho Noria Aguilarena, N of Ures and Santiago, 29°33'N, 110°25–26'W, 500 m, 9 Jul 1992, E. Joyal 2054 (ARIZ); Cañon de la Bota, N end of Sierra el Tigre, 34 km (air) ESE of Esqueda, near 30°36'N, 109°13'W, 3300–3600 ft., 31 Jan 1982, sterile specimen, G. Yatskievych 82-54 (ARIZ); 15 miles SE of Magdalena to Cucurpe, 3200–3300 ft, 21 May 1963, R. S. Felger 7942 and H. S. Gentry (ARIZ); 17 miles SE of Magdalena, Palm Canyon in Cerro Cinta de Plata, 5 Jun 1978, T. R. Van Devender s.n. (ARIZ); 15 miles SE of Magdalena, 3000–3400 ft, 21 May 1963, R. S. Felger and H. S. Gentry 19988 (ARIZ); 17 miles SE of Magdalena, 11 Sept 1934, I. L. Wiggins 7132 (ARIZ).

4. *Hesperaloe parviflora* (Torrey) J. M. Coulter, Contributions from U.S. National Herbarium. 2:436. 1894.—*Yucca parviflora* Tor-

291

rey, Botany of the Boundary of Emory's Report of the U.S. and Mexican Boundary Survey, 221. 1859.—*Aloe yuccaefolia* A. Gray, Proceedings of the American Academy of Arts and Sciences, 7:390. 1867., illegit., based on *Hesperaloe parviflora* (Torrey) J. M. Coulter.—*Hesperaloe yuccaefolia* (A. Gray) Engelmann, in C. King, Geological Exploration of the 40th Parallel, 5, 497. 1871., illegit., see preceding.—SYNTYPES: USA, Texas; "Gravelly hills near the mouth of the Pecos", *Bigelow s.n.* Stony hills west of the Nueces river, *Wright 1908.* (lectotype: GH!; isolectotype: NY!)

Hesperaloe engelmanni Krauskopf, Notice to Botanists. (circular). 1878.—TYPE: none designated. Hesperaloe parviflora (Torrey) Coulter [var.] engelmanni (Krauskopf) Trelease, Annual Report of the Missouri Botanical Garden, 13:33. 1902.—TYPE: none cited; placed in synonymy here; see discussion under taxonomy.

Plants densely caespitose, forming clumps to 1 m or more wide. Leaves dark green, arching, 30-60 (120) cm long, 8-18 mm wide at base, narrowing to apex, linear, margin finely filiferous, with tightly curled fibers. Inflorescence branched panicle to 1-2.5 m long, the few branches mainly in upper one-half. Flowers diurnal, tubular or oblong-campanulate, in indeterminate fascicles; tepals salmon, coral, pink, or rosy-red, one horticultural selection is yellow, the outer 15-20 mm long, 4-7 mm wide, the inner 17-20 mm long, 5-8 mm wide; stamens included, the filaments 7-13 mm long, attached to base of tepals for 1 mm, anthers 2–3 mm long; ovary 4–6 mm long, 3-4 mm wide at anthesis, style included. Capsule ovoid or oblongovoid, 30-40 mm long, 25-30 mm wide, beaked, long pedunculate, rugose; seeds black 9-10 mm long, 6-7 mm wide. Hesperaloe parviflora occurs in Larrea desert, oak and chaparral zones from 600-2000 m in northwestern Coahuila, and Val Verde, Mills, San Saba, Haskell and Collin Counties in Texas.

Phenology and distribution (Fig. 1). Flowering period for *Hesperaloe parviflora* ranges from March through September. The species is known from central Texas in the Edwards Plateau region and adjacent Mexico.

Taxonomy. In 1859, Torrey described Yucca parviflora from gravelly hills near the mouth of the Pecos (*Bigelow s.n.*) and stony hills west of the Nueces, Texas (*Wright 1908*). Then in 1867, Gray decided that the taxon fit into Aloe better than Yucca and described Aloe yuccaefolia. Gray used Wright 685 with flowers and mature fruit and Wright 1908, the same collection used by Torrey for his description of Yucca parviflora. Gray (1867) used the specific epithet of yuccaefolia because there was already an Aloe parviflora. In 1871, Engelmann created the genus Hesperaloe and transferred the recently described *Aloe yuccaefolia*. However, *Yucca parviflora* has priority making the correct combination *Hesperaloe parviflora* (Torrey) Coulter. Krauskopf (1878) proposed the name *Hesperaloe engelmanni* for plants with longer anthers and a short, thick (not filiform) style. These plants were collected along the western branch of the Nueces river while the plants Wright collected came from near the Nueces river and Devil's river. These localities are close enough that neither specific nor subspecific rank should be maintained for those plants until more field research can be done.

Specimens examined. USA. Texas: Mills Co., 1 mile W of Center City on route 84, 27 May 1964, C. E. Smith Jr. and H.-S. Gentry 4322 (ARIZ); MEXICO. Coahuila: ca. 12 air miles E. of Boquillas, 83 road miles NW of Rancho El Jardin, 29°10'N, 102°44'W, 27 July 1973, J. Henrickson 11488 (ARIZ); Los Cojos Minas, SW slope of Sierra del Carmen, 11 October 1972, R.G. Engard and H.S. Gentry 23118 (ARIZ).

5. Hesperaloe tenuifolia G. D. Starr sp. nov. (Fig. 4)—TYPE: MEXICO, Sonora; 24 km (airline) northeast of Alamos, near Rancho Santa Barbara on Cerro Agujudo, 108°43'43"W, 27°06'50"N, elevation 1500 m, 16 May 1990, *S. Meyer and P. Jenkins 9063* (holotype: ARIZ!)

Planta acaulis, cespitosa, 0.5 m lata; foliis linearis-longiapiculatis, 0.5–1 m longis, 0.5–1 cm latis ad basim, margine angusto sparse filifero; inflorescentia paniculata, 1.5–2 metralis; flores pedicillati, tepala exteriora dorsaliter rosea mediane brunneo-virido ventraliter albida margine rubro, interiora dorsaliter obscure rosea margine albo ventraliter albida, 15 mm longa, 3 mm lata; antheris inclusis, capsulae ovoideae, 2–3 cm longae, 2–2.5 cm latae; semina nigra 6–9 mm longa, 5–6 mm lata.

Plants acaulescent, sparsely caespitose, forming small clumps to 0.5 m wide. Leaves arching, narrowly linear 0.5–1 m long, 0.5–1 cm wide at the base tapering to the apex, margins thin, finely filiferous, fibers white and not tightly curled. Inflorescence raceme or 2–3 branched panicle, to 1.5–2 m long. Flowers nocturnal, rotate; outer tepals linear, 13 mm long, 5 mm wide, dorsal side dark pinkish-red, ventral face white with reddish margin; inner tepals ovate, 15 mm long, 8 mm wide, dorsal side dark pinkish-red with white margin, ventral face white; anthers included, attached to base of tepals for 2 mm, filaments 9 mm long, anther sacs 3 mm long; ovary 6 mm long, 3 mm wide, style 4 mm long. Capsule ovoid, 2–3 cm long, 2–2.5 cm wide, beak none or to 1 mm long; seeds black, 10 mm long, 5–7 mm wide.

Phenology and distribution (Fig. 1). Flowering occurs primarily in April and May with seed maturing in June and July. *Hesperaloe*

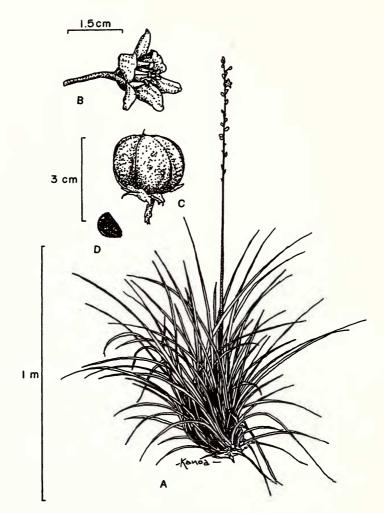


FIG. 4. Hesperaloe tenuifolia A. Habit. B. Flower. C. Capsule. D. Seed.

tenuifolia is known only from the Cerro Agujudo northeast of Alamos, Sonora. Plants grow on rhyolitic rock on dry hilltops at 1500 m with *Pinus oocarpa, Pinus leiophylla*, and *Quercus tarahumara*.

HORTICULTURE

Hesperaloe has been cultivated in the United States since at least 1878 when Krauskopf offered for sale plants that he collected along the western branch of the Nueces River in western Texas. Prior to that, plants were grown at the botanical gardens in Cambridge from

294

material Wright collected in 1849. All species are best used in full or reflected sun, and a fast draining soil. The growth rate varies from fast (flowering in 4 years from seed) to moderately fast (flowering in 5 years from seed). The fast growing species are H. parviflora and H. tenuifolia, and the slower growing species are H. campanulata, H. nocturna, and H. funifera. Hesperaloe has CAM metabolism so growth occurs year round. Because of this, they can be grown faster by applying fertilizer and consistent, thorough waterings all year. Amount of fertilizer and water applied will vary with temperature though. All species are quite drought tolerant once established. They will survive on less than 12" of annual precipitation and can go for 2 months or more without supplemental water. No maintenance is required except for removal of old flower spikes if so desired. All species are hardy to at least 15° F with H. funifera and H. parviflora being hardy to at least 10° F. The flowering period for all species is usually longer for cultivated plants than for wild populations. The application of supplemental water and the warmer temperatures of cities versus the open desert results in flower spikes appearing earlier and persisting later in the year. The flowers of H. parviflora are visited by hummingbirds as well as bees. Flowers of H. funifera, H. nocturna, and H. tenuifolia are visited by bats and hawk moths. Hesperaloe campanulata flowers are visited by bats and hawk moths at night, and visited by hummingbirds and bees by day.

Hybrids

Hybrids in Hesperaloe are known to occur. Hybrid plants that were results of the crosses H. nocturna \times H. parviflora (pollen parent undetermined) and H. parviflora (male) \times H. funifera (female) have been observed. F_2 offspring from the *H. parviflora* \times H. funifera hybrid plants have also been observed. These plants were still young, however some were of flowering age and did show segregation of flower characteristics back towards the parent species. The progeny of H. nocturna \times H. parviflora had the flower color of *H. parviflora* and flower shape intermediate, while the leaves were more like H. nocturna. I have made crosses between H. campanulata (male) \times H. funifera (female) and H. campanulata (male) \times (*H. parviflora* \times *H. funifera*) (female). I made the *H. campanulata* \times H. funifera cross after visiting the unusual H. funifera population in western Nuevo Leon. The proximity to both H. campanulata and H. funifera, along with the variation in flower color within this population, gave me the impression that the plants were of hybrid origin. It is also possible that these plants are the result of a H. parviflora \times H. funifera cross. However, all the flowers had tepals that were flared open like H. funifera, whereas I would expect to see flowers

similar to both parents in a segregating population. It seems unlikely that these could be F_1 plants because there are no known populations of *H. parviflora* in the vicinity. Seed has been collected and plants are being grown to further study this variant of *Hesperaloe. Hesperaloe campanulata* also is of possible hybrid origin. *Hesperaloe funifera* and *H. parviflora* may have crossed at some point in the past and *H. campanulata* and the unusual plants in western Nuevo Leon could be descendants of that cross. In the field, flower color and shape of *H. campanulata* were consistent, while leaf size was variable. This leads me to conclude that *H. campanulata* is a stable species. However, the population of *H. funifera* in western Nuevo Leon appears to be simply a color variation and therefore not recognizable as a distinct taxon.

ACKNOWLEDGMENTS

I thank Dr. Steve McLaughlin for his encouragement, manuscript review, and for sharing his extensive knowledge of *Hesperaloe*. I thank Mr. Ron Gass for his enthusiasm in the field and continued support throughout this project. I also thank Dr. Charles Mason for his taxonomic help and manuscript review. My thanks go out to Dr. Richard Felger for scrutinizing the manuscript. Thank you also to Dr. George Yatskievych for his tireless research into the taxonomy of *H. funifera*. Many thanks to Dr. Marshall Johnston for his review of the Latin diagnoses. Also, I thank Kim Duffek and Anne Gondor for their illustrations and Phil Jenkins for his herbarium help and many suggestions. Finally, many thanks to Wendy Hodgson for her illustrations and invaluable herbarium help.

LITERATURE CITED

- BAKER, J. G. 1898. On Aloineae and Yuccoideae. Journal of the Linnean Society of Botany 18:228.
- COULTER, J. M. 1894. Botany of Western Texas. Contributions from the U.S. National Herbarium 2:588 pp.

ENGELMANN, G. 1871. *In* S. Watson (ed.), U.S. Geological Exploration of the 40th Parallel. Report of the 40th Parallel, Vol. 5:525 pp.

- GENTRY, H. S. 1967. A new *Hesperaloe* from Sonora, Mexico. Madroño 19(3):74-78.
- KOCH, K. 1862. Exposition quinquennale de plantes et de fleurs Belgique Horticole 12:107–133.

KRAUSKOPF, E. 1878. Notice to botanists, botanical gardens and nurserymen. Circular.

LEMAIRE, C. 1864. Especes Nouvelles D'Agave. L'Illustration Horticole 11:63-66.

LEMAIRE, C. 1866. Du Genre Yucca. L'Illustration Horticole. 13:90-102.

TORREY, J. 1859. Botany of the boundary; Emory's report of the U.S.-Mexican Boundary Survey. 29-270.

TRELEASE, W. 1902. The Yucceae. Report of the Missouri Botanical Garden 13:27-31.

296

NOTES

THE MONOTROPOIDEAE IS A MONOPHYLETIC SISTER GROUP TO THE ARBUTOIDEAE (ERI-CACEAE): A MOLECULAR TEST OF COPELAND'S HYPOTHESIS. Kenneth W. Cullings, Department of Biology, San Francisco State University, San Francisco, CA 94132 and Lena Hileman, Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138.

The Monotropoideae (Ericaceae) is a group of plants, mostly California natives, with an achlorophyllous, mycotrophic habit; all plants in this subfamily depend upon shared mycorrhizal connections with neighboring photosynthetic plants for carbon nutrition (Björkman, Physiologia Plantarum 13:309–327, 1960). These associations can be quite specific; the most specific mycorrhizal association of any kind is between *Pterospora andromedea* and the mycorrhizal fungus *Rhizopogon* (Cullings et al., Nature 379:63–65). The morphology and physiology of these symbioses can be defining characters in the taxonomy of the Monotropoideae and related subfamilies of the Ericaceae (Cullings, Journal of Evolutionary Biology 7:501–516, 1994; Cullings et al., Nature 379:63–65, 1996), and detailed molecular analysis of relationships among members of the Monotropoideae with respect to these characters has been described (Cullings, Journal of Evolutionary Biology 7:501–516, 1994).

Both morphological (Copeland, Madroño 6:97–119, 1941; Wallace, Bot. Notiser 128:286–298, 1976) and molecular evidence (Cullings and Bruns, Canadian Journal of Botany 70:1703–1708, 1992; Cullings, Journal of Evolutionary Biology 7:501–516, 1994) strongly indicate that the bulk of the Monotropoideae share a most recent common ancestor with the Arbutoideae (Ericaceae). However, morphological hetero-geneity prompted Copeland (Madroño 6:97–119, 1941) to hypothesize that the Monotropoideae may be polyphyletic within the Arbutoideae. Recently, Cullings (Journal of Evolutionary Biology 7:501–516, 1994) provided strong molecular evidence that one monotropoid species, *Monotropsis ordata*, is in fact most closely related to members of the Vaccinioideae, and that the Monotropoideae is polyphyletic. Furthermore, this study confirmed the close association between the bulk of the Monotropoideae was limited to two *Arctostaphylos* species, Copeland's hypothesis that the Monotropoideae has more than one origin within the Arbutoideae has not been fully addressed using molecular methods.

In this study, partial 28S nuclear ribosomal RNA (nrRNA) gene sequences were used to test Copeland's hypothesis. Sequences were generated using the polymerase chain reaction (PCR) and plant-specific primers developed by Cullings (Molecular Ecology 1(4):233–240, 1992). PCR products were sequenced directly using the asymmetric primer ratio method (Gyllensten and Erlich, Proceedings of the National Academy of Sciences U.S.A. 85:7652–7658, 1988) and resulted in 500 bases of easily alignable sequence with 2 small indels that were omitted from the analysis. Data were analyzed cladistically using PAUP vers. 3.1.1 (Swofford, D. L. Computer program distributed by Illinois Natural History Survey, Champaign, III, 1995), and by neighbor-joining using PHYLIP vers. 3.572. All analyses were performed with characters unweighted, and bootstrapping was used to assess strength of clades. Trees were rooted by the outgroup comparison with *Clethra* (Clethraceae, Ericales).

Results of this study indicate that the Monotropoideae and Arbutoideae are monophyletic sister groups (Fig. 1), and thus do not support Copeland's hypothesis that the bulk of the Monotropoideae are polyphyletic within the Arbutoideae. Relationships within the Monotropoideae depicted by parsimony analysis of 28S rRNA data have been reviewed previously, and are supported by both morphological and bio-

MADROÑO, Vol. 44, No. 3, pp. 297-304, 1997

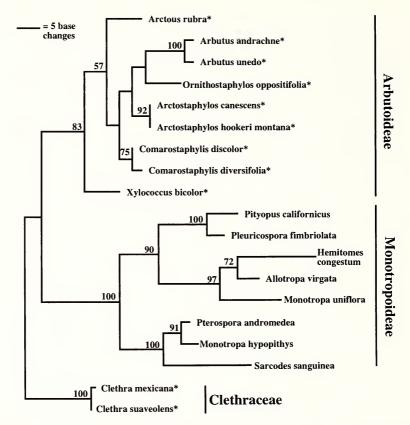


FIG. 1. Phylogeny of the Arbutoideae and Monotropoideae based on partial 28S ribosomal RNA gene sequences. Analysis resulted in a single most parsimonious tree with length: 234, C.I.: 0.709, R.I.: 0.796, rescaled C.I.: 0.565. Numbers at nodes are bootstrap indices of support (1000 replicates). New sequences are indicated by *, all others have been published previously (Cullings, Journal of Evolutionary Biology 7: 501–516, 1994). Tree is drawn to scale shown.

chemical data (Cullings, Journal of Evolutionary Biology 7:501–516, 1994). Relationships within the Arbutoideae are unresolved by these data (Fig. 1); genera are well supported as monophyletic, but relationships among genera could not be resolved. These relationships are currently being determined using the internal transcribed spacer (ITS), a more rapidly evolving portion of the rRNA repeat unit (Jorgenson and Cluster, Annals of the Missouri Botanical Garden 75:1238–1247, 1988).

Taken together, molecular data provide a comprehensive picture of evolutionary patterns within a broadly defined Ericaceae. Both nuclear (28S rRNA) and chloroplast (rbc-L) data indicate that the Arbutoideae split from the Ericaceae relatively early, and that the ericoid mycorrhiza-formers, a group that includes the bulk of the Ericaceae, plus the Empetraceae and Epacridaceae (Kron and Chase, Annals of the Missouri Botanical Garden 80(3):735–741, 1993; Cullings, Canadian Journal of Botany in press), form a derived group relative to the Arbutoideae. Nuclear data provide further resolution, and indicate that the Ericaceae split into two main groups, the

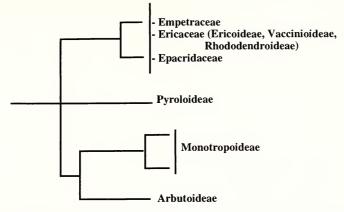


FIG. 2. Schematic of evolutionary trends within the Ericaceae based on a consensus of chloroplast (rbc-L) and nuclear (28S rRNA) DNA data. Tree indicates that the arbutoid and monotropoid mycorrhiza-forming groups, Arbutoideae and Monotropoideae, form a monophyletic sister group to the ericoid and pyroloid mycorrhiza-formers, and that the position of the Pyroloideae is unresolved by molecular data.

arbutoid/monotropoid mycorrhizae formers, a clade consisting of the Arbutoideae and Monotropoideae, and the ericoid mycorrhiza-formers (Cullings, Journal of Evolutionary Biology 7:501-516, 1994) (Fig. 2). The Pyroloideae, a group that forms mycorrhizae that are intermediate in form, cannot be placed within either clade. Based on this, it appears that one of the pressures influencing cladogenesis within the Ericaceae may have been nutrient access via different mycorrhizal strategies, with the ericoid mycorrhiza clade liberating nutrients from acidic soils (Cullings, Journal of Evolutionary Biology 7:501-516, 1994; Specht, Heathlands and Related Shrublands, R. L. Specht (ed.), Elsevier Scientific Publishing Company, New York, 1977), and the arbutoid/monotropoid clade receiving carbon through mycorrhizal connections with ectomycorrhizal fungi shared in common with neighboring trees. Members of the Monotropoideae have taken this strategy to the extreme, and have become achlorophyllous and wholly dependent upon these shared mycorrhizal connections (Björkman, Physiologia Plantarum 13:309-327, 1960: Cullings et al., Nature 379:63-65, 1996). However, because the Monotropoideae are achlorophyllous, it is likely that much of their chloroplast genome has been reduced or lost, as in the case of the achlorophyllous plant parasites in the Orobanchaceae (dePamphilis et al., Nature 348: 337-339, 1991). Thus, corroborating data from chloroplast DNA may not be possible with rbc-L, though other chloroplast loci may prove useful. At present this possibility is being explored.

Setaria tenax (Rich.) Desv. (Panicum tenax Rich.) is a neotropical perennial in the subgenus Setaria that ranges from southern Mexico to northern South America. The type (FI; fragment, US!) was collected in Cayenne, French Guiana. Within its range, S. tenax is best distinguished from its congeners by the following combination of characters: the awns subtending the spikelets bear both antrorse and retrorse barbs; the spikelets are 2.2–2.5 mm long and somewhat hemispheric; the first glume is one-

LECTOTYPIFICATION OF SETARIA TENAX VAR. ANTRORSA (GRAMINEAE).—Laurence J. Toolin, Herbarium, Shantz 113, University of Arizona, Tucson, AZ 85721.

third as long as the spikelet, and the second glume is about one-half the spikelet length; the fertile lemma is strongly gibbous, transversely rugose below, becoming smooth and shiny at the apex.

In 1962 (Illinois Biol. Monogr. 29, p. 44.), J. M. Rominger described a variety, *antrorsa*, of *Setaria tenax*. He indicated the type locality as Chichén Itzá, Yucatán, Mexico, citing *Swallen 2439*, with specimens deposited at both MO and US, but did not designate either of the specimens as the holotype. He noted that his new variety differed from var. *tenax* solely in having only antrorse barbs on the awns, with no retrorse barbs present. Var. *antrorsa* is known from the Mexican states of Yucatán, Veracruz, and Chiapas, as well as Honduras (R. W. Pohl, Flora Mesoamericana 6: 360. 1994).

The US specimen of *Swallen 2439* was examined as part of a study comparing some North and South America taxa to verify the occurence of certain species in both hemispheres. It was noticed immediately that Rominger had never annotated the sheet, and this had been noted on the specimen by D. H. Nicholson. The US folder is labeled "possible isotype". The MO specimen also has no annotation by Rominger. The MO sheet was annotated as an isotype by G. Davidse, who may have simply assumed that the holotype was at US. Pohl (*l.c.*), who seems to be the only author to deal with var. *antrorsa* since Rominger, states the following: "Holotipo: Mexico, Yucatán, *Swallen 2439* (US!)." Pohl is obviously incorrect here, since Rominger himself did not select the US specimen as holotype, and, moreover, listed MO ahead of US in citing the type specimens. How Pohl came to consider the US specimen to be the holotype is a mystery. Rominger, in a recent conversation, told me that he had never had any discussion with Pohl regarding var. *antrorsa*, and encouraged my selecting a lectotype. Pohl's published citation, left uncorrected, constitutes a potential source of confusion.

Article 9.9 of the Tokyo *Code* (1994) provides for the lectotypification of a taxon where a holotype is not designated in the original protologue. Lectotypification of *Setaria tenax* var. *antrorsa* is therefore proposed here.

The MO and US specimens of var. *antrorsa* are not of equal quality. The US sheet has a single culm with an immature panicle. The young spikelets are not mature enough to exhibit adequately the *Setaria tenax* characters given above. The MO specimen, in contrast, has two mature panicles in which the spikelets are well-developed and typical of the species. Because the latter specimen clearly better represents the species, and because Rominger cited the MO specimen first in his protologue, I designate *Swallen 2439* at MO (sheet No. 1043993) as the lectotype of *Setaria tenax* var. *antrorsa*; the US specimen (sheet No. 3090500) then becomes the isolectotype.

REPRODUCTIVE RESPONSE TO FIRE BY THE LAUREL SUMAC, *MALOSMA LAURINA* (ANACAR-DIACEAE).—Gary B. Perlmutter, 151 N. Lomita Avenue, Ojai, CA 93023.

One of the adaptations perennial plants have to an environment with frequent fires or other stresses is the ability to sprout from surviving structures within the soil after the aerial portions have been destroyed by the disturbance. These subterranean features include rhizomes, bulbs, and undamaged root crowns. Many such fire resistant species produce flowers either immediately following or more than two years after the plant is burned (Gill, Fire and the Australian Biota, Australian Academy of Science, Canberra, 1981; Platt et al., Occologica 76:353–363, 1988).

Malosma laurina (Nutt.) Abrams (laurel sumac) is a facultative resprouter (Saruwatari and Davis, Oecologica 80:303–308, 1989) with year-round growth in coastal environments of southern California (Watkins and de Forest, Ecology 22:79–83, 1941). While its growth patterns and seedling survivorship following fire disturbance have been studied (Thomas and Davis, Oecologica 80:309–320, 1989), the repro-

NOTES

ductive effects of this species have been overlooked. Is flowering hindered by vegetative growth in burn recovery or do plants flower the following summer regardless of canopy damage by a recent fire? The data presented here aim to answer this question.

Phenological patterns of inflorescences of burned and unburned sumacs were studied in habitats of similar climate along coastal slopes of the Santa Monica Mountains $(34^{\circ}05'N, 119^{\circ}02'W)$ in southeastern Ventura County. The climate is of the South Coast Thermal Belt with mild winters and summer heat modified by marine influence (Hickman, The Jepson manual: higher plants of California, University of California Press, 1993). One of these sites was burned by the Green Meadow Fire in October 1993 while two others were spared by the fire. Reconnaissance of the area for site selection in November 1994 revealed sprouting shrubs about 1 m tall scattered throughout a successional grassland except for a few patches of unburned coastal sage scrub where large *M. laurina* shrubs flourished. Site descriptions are as follows:

The burned site lies at the Mugu Peak trailhead at the base of a southwest-facing slope at 6 m elevation. The plant community was a successional grassland dominated by Nassella sp., M. laurina, and Malacothamnus fasciculatum. The soil was a pebbly loam with a water capacity of 0.43 cm/cm. Malosma shrubs were stump-sprouting, with conspicuous burnt branches extending beyond the living canopies. Down the coast, 4 km ESE from this site is the site Unburnt 1. Also at 6 m elevation, it lies at the base of a south-facing slope just east of La Jolla Canyon. The community is Diegan Coastal Sage Scrub (Holland, Preliminary descriptions of the terrestrial natural communities of California, California Department of Fish and Game, 1986) dominated by Artemesia californica, M. laurina, and Salvia mellifera. Malosma canopies were interwoven to form a nearly continuous horizontal band at that altitude for 1 km. The soil is a fine sandy/silty loam with blocky talus and 0.13 cm/cm water capacity. The site Unburnt 2 lies 8 km ESE of the burned site, along Deer Creek Rd at 150 m elevation on a northeast-facing slope. This was in a low, 1 m high chaparral dominated by Lotus scoparius, Ceanothus megacarpus, and M. laurina. Although the community structure and composition suggests second-year fire succession (McAuley, Wildflowers of the Santa Monica Mountains, Canyon Publishing Co., 1985), study shrubs showed no fire damage. The soil was a gravelly loam with 0.46 cm/cm water capacity.

At each site, five representative individuals at least 2 m tall were selected for study and marked with flagging. Beginning in May 1995, sites were visited weekly to record the presence and condition of inflorescences at each plant. Panicle condition was classified and ranked into the following stages: growing buds (1), mature buds (2), and flowers (3). The growing bud stage is characterized by a reddish color and small size; the mature bud stage exhibits greenish, pinkish or whitish color and larger size. Each plant canopy was divided into four sections (north, east, south, and west faces) to bring the sample size to 20 per site; in each section I recorded the stages panicles were observed in.

From the data, onset and peak dates of each stage were determined and compared among sites, as were flower development periods (D_{Fl}), which is here defined as the number of weeks from the date of first buds observed to the date when at least 50% of a population is in flower (Bowers, Madroño 43(1):69–84). Stage onset dates of each shrub were further compared to assess within-site variation.

Burned shrubs showed no panicles from previous seasons, whereas inflorescences were abundant on unburned plants. Onset and peak dates of bud and flower stages were up to 5 wk later among burned shrubs (Fig. 1); however, D_{F1} was 8 wk in each site.

Within sites, onset dates of individual shrubs varied 1-4 wk (Fig. 2). In the burned site, this variance for the growing bud, mature bud and flower stages are 4, 3, and 1 wk, respectively; in Unburnt 1 these are 1, 4, and 4 wk; and in Unburnt 2 they are 2, 4, and 3 wk.

In the burned site, Malosma laurina resprouters did not produce flowers until two

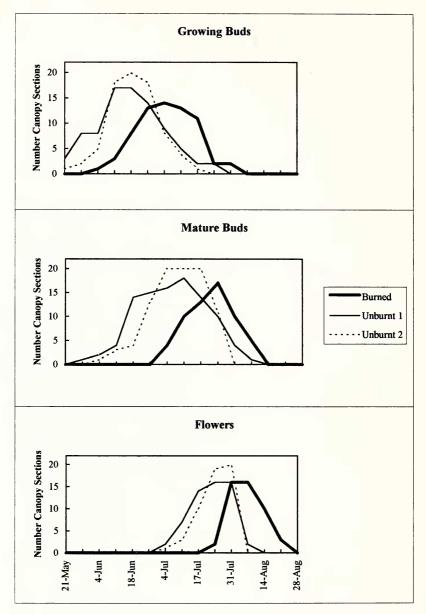
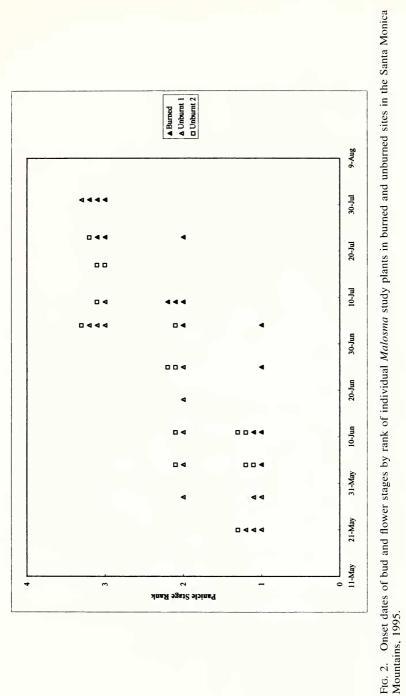


FIG. 1. Phenograms of burned and unburned study populations of *Malosma* in the Santa Monica Mountains, 1995 ($n_i = 20$).



years after the fire, when plants approached 2 m height. Many fire resistant shrubs in Australia have a similar response (Gill, 1981). Flowering in this species seems to be related to plant vigor, which could be indicated by shrub size or time of recovery. As for size, Florida scrub plants had to attain a minimum stem diameter before producing flowers after a fire (Ostertag and Menges, Journal of Vegetation 5:303– 310, 1994). This seems unlikely for *Malosma*, since the sizes of burned shrubs varied (1.5–2.5 m height by 1.5–4.0 m width, estimated). Canopy sizes were observed to be in direct proportion to their extended burned branches (no data collected), which is likely proportional to the sizes of their root crowns. Furthermore, the delay period of two years by resprouters did not vary, which suggests that a certain amount of time is required for these shrubs to recover in order to make a reproductive effort.

This second year response among burned shrubs, plus the observed delay in the development of inflorescences as compared to the unburned populations, could be explained by the investment of energy toward vegetative growth in fire recovery. Throughout the season this growth was observed in all study plants, and more pronounced among resprouters (no data collected). Two earlier studies of *M. laurina* populations in the Santa Monica Mountains illustrate a drastic increase in vegetative growth by resprouting shrubs. During the primary growing season from February through July, Thomas and Davis (1989) reported shoot elongation of 16 cm per month by resprouters in the first year after a fire. This is about ten times the growth rate of that reported for undisturbed shrubs (1.8 cm per month) during the same period by Watkins and de Forest (1941).

Alternatively, the delay in panicle emergence and development could be explained by population genetics. Each study population is separated by a distance of 4 km, which make it unlikely for these populations to interbreed, due to the foraging patterns of their insect vectors. However, *Malosma* shrubs were found throughout the areas between sites, thus being part of a larger contiguous population. The reconnaissance visit in 1994 revealed morphological similarity among resprouters (i.e., no panicles observed at one year after fire) at Pt. Mugu, La Jolla Canyon, Sycamore Canyon, and along Deer Creek Rd. Therefore, it seems unlikely that the burned population exhibited phenological patterns that were unique to that population. A genetic analysis of selected plants in these locations could reveal how similar the above populations are.

As the within-site variation of bud and flower onset indicate, the observed withinseason delay of the burned population is not significant. The greater number of onset dates shared by shrubs in the burned site and Unburnt 2, which have similar soil water capacities, than the former and Unburnt 1, where these are different, suggests that soil moisture also influences timing and development of flowers, but to a lesser degree than fire disturbance.

I am grateful to Dieter H. Wilken of the Santa Barbara Botanic Garden for his advice throughout the study. I also wish to thank Ray Sauvajot of the National Park Service, David A. Young, and an anomynous reviewer for their helpful comments to earlier drafts of the manuscript, while Steven G. Lawry of Lawry's Technical Services provided transportation to and from sites. Fieldwork was conducted under a Research Permit issued by the Santa Monica Mountains National Recreation Area with verbal permission from Point Mugu State Park.

NOTEWORTHY COLLECTIONS

CALIFORNIA

DODECAHEMA LEPTOCERAS (A. Gray) Rev. & Hardham (POLYGONACEAE).—Riverside Co., between 13 and 16.2 km E of Temecula, S of Vail Lake, in and adjacent to the Arroyo Seco and Kolb Creek drainages, 455 to 550 m, in Temecula Arkose formation, 5 May 1989, Gordon-Reedy s.n. (SD). Bare or sparsely vegetated benches above drainages, openings in chaparral, or understory (leaf litter) of oak trees. Associated species: Adenostoma fasciculatum, Adenostoma sparsifolium, Eriogonum fasciculatum ssp. foliolosum, Eriastrum sappharinum, Stylocline gnaphalioides, Vulpia myuros var. hirsuta, Chorizanthe coriacea, Salvia columbariae, Nemacladus longiflorus, Lupinus bicolor, and Chaenactis glabriuscula.

Previous knowledge. Dodecahema leptoceras had an historical distribution along the southern margin of the San Gabriel, San Bernardino, and San Jacinto mountains, where it was documented on sandy, flood-deposited river terraces and washes below about 670 m, in association with intermediate to older successional phases of alluvial scrub habitat. Although this species had been recorded from over 20 localities, only 5 extant sites were known prior to this occurrence, and most of these were relatively small (<2000 individuals) and/or unprotected.

Significance. The Vail Lake population represents (1) a new location for this federally and state-endangered species, (2) a southward range extension of approximately 25–27 km from the nearest known locality along Bautista Creek, (3) the largest known population, and (4) an occurrence in "atypical" habitat. Population size was estimated at approximately 10,000 individuals in 1989. Re-surveys of the area in 1990 revealed population increases at most locations, for a revised population estimate of 19,000 individuals. A portion of the population occurs on U.S. Forest Service land, thereby receiving some degree of protection. While part of the population occurs in typical floodplain habitat (i.e., benches above the main drainage), the remainder of the population occurs in upland habitat or dry drainages not associated with a well-developed floodplain. Habitat along Arroyo Seco and Kolb creeks includes alluvial sage scrub and Riversidian sage scrub; associated habitat in upland areas includes southern mixed chaparral, chamise chaparral, redshank chaparral, and a coast live oak/southern mixed populations of this endangered species.

—PATRICIA GORDON-REEDY, Ogden Environmental and Energy Services Co., San Diego, CA 92121.

CARDAMINE FLEXUOSA With. (BRASSICACEAE).—San Diego Co.: San Diego, Balboa Park, scattered weed in plantings outside and inside Botany Building; several dozen plants seen, 29 January 1997, *M. A. Vincent 7670* (MO, MU, RSA, SD); San Diego Co.: Balboa Park, San Diego Zoo, very common weed in wet area along retaining wall below large aviary; hundreds of plants, 29 January 1997, *M. A. Vincent 7677 & J. Solomon* (MU, RSA, SD, UC).

Previous knowledge. This European native has been reported for several states in eastern and central North America (R. C. Rollins, 1993, Cruciferae of Continental North America, Stanford Univ. Press, Stanford). It is a weed of moist areas and gardens, and is often found in recently planted beds or in pots with potted plants.

Significance. New for California. In The Jepson Manual (R. C. Rollins, 1993,

MADROÑO, Vol. 44, No. 3, pp. 305-307, 1997

Cardamine, in J. C. Hickman [ed.], The jepson manual: higher plants of California, Univ. Calif. Press, Berkeley), *C. flexuosa* will key out with *C. pensylvanica, C. hirsuta*, and *C. oligosperma*, annuals or biennials from fibrous roots or weak taproots. In California, *C. flexuosa* blooms in December–January, while the other species bloom mid- to late spring. A modified key for these four taxa follows, which would fall under the first lead of couplet 6:

1.	Basal lvs 0-few, gen not rosetted, gen deciduous; lower st hairs few or gen 0
	2. Lflets and lobes decurrent on rachis, broadly oval to oblong; sts erect, not
	flexuous C. pensylvanica
	2' Lflets and lobes petiolate, oval to orbicular; stems flexuous C. flexuosa
1'	Basal lvs several-many, gen \pm rosetted, persistent; lower st hairs 0 or gen many
	3. Sts 1-many, erect, 5-30 cm, outer 0 or decumbent; fr ≤ 1 mm wide
	C. hirsuta
	3' Sts 1-several, erect to ascending, gen ≥ 20 cm; fr 1-2 mm wide

--MICHAEL A. VINCENT, W.S. Turrell Herbarium, Department of Botany, Miami University, Oxford, OH 45056. Vincenma@muohio.edu

GAURA PARVIFLORA L. (ONAGRACEAE).—San Bernardino Co., Montclair, N side of I-10 at W side of Benson Ave., between Central and Mountain Avenues, 34°05.5'N, 117°41'W; T1S R8W S14, alt. 350 m, locally common in dense colonies in a disturbed weedy area, 30 May 1996, *A. C. Sanders 18192* (UCR, and to be distributed); 9.5 km N of Crossroads, Colorado River [near Parker Dam], 23 Apr. 1940, *A. M. Alexander and L. Kellogg 1213* (RSA).

Previous knowledge. Native to the central U.S. and common west to Arizona. Very scarce in California, previously reported only from "SW" without definite locality by W. L. Wagner (*in* J. C. Hickman, ed., The Jepson manual: higher plants of California, Univ. of Calif. Press, 1993) and specifically from Orange (P. A. Munz, A flora of Southern California, Univ. of Calif. Press, 1974) and Santa Barbara (C. F. Smith, A flora of Santa Barbara region, California, Santa Barbara Mus. of Nat. Hist., 1976; Munz 1974) counties. Raven and Gregory in their *Gaura* monograph (Mem. Torr. Bot. Club, 23(1):1–96, 1972) did not cite specific collections of this species in the U.S., but did provide a map with small dots indicating collection sites. There are three dots shown in California, one of which doubtless refers to the Crossroads locality cited above. They did see this collection because the RSA duplicate was annotated by them. This earlier dot reference to this collection has evidently been overlooked because neither San Bernardino County nor the California deserts are included within the range of this species in subsequent floristic works (Munz 1974; Wagner 1993).

Significance. First specific records from San Bernardino County and the deserts of California, and first collection since 1956 in California, based on specimens at RSA and UCR. The Crossroads locality may represent the western fringe of the species' natural range, but the coastal slope localities certainly represent introduced populations. The Montclair locality is ca. 25 km NE of a previous locality in Brea, Orange County. This species should be sought at other localities in southern California. It has probably been continuously present since the 1940s but overlooked, despite its 2–3 m stature, because few collectors work on urban weeds.

—ANDREW C. SANDERS, Herbarium, Dept. of Botany and Plant Sciences, University of California, Riverside, CA 92521.

CREPIS TECTORUM L. (ASTERACEAE).—San Bernardino Co., San Bernardino Mtns., Snow Summit Ski area, T2N R1E S28, alt. 2200 m, 20 Sep 1985, *Tim Krantz s.n.* (UCR); Mono Co., Mammoth Lakes, 37°38.8'N, 118°58.8'W, alt. 2470 m, uncommon in one local area on roadside among pines, 26 Sep 1996, *George Helmkamp 1218* (UCR). (Krantz collection determined by John Strother.)

Previous knowledge. Native to Eurasia, previously naturalized in Minnesota and at scattered locations in the Northeast (Gleason, H. and A. Cronquist, Manual of vascular plants of northeastern United States and adjacent Canada, 2nd ed., 1991). *Significance*. First records for California.

—ANDREW C. SANDERS, Herbarium, Dept. of Botany and Plant Sciences, University of California, Riverside, CA 92521.